

# CANOTIA

## VOLUME 14

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# CANOTIA

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**Canotia** is named for *Canotia holacantha* Torr. (Celastraceae), a spiny shrub or small tree nearly endemic to Arizona.

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**FOUR STUDENTS REMEMBER THEIR MENTOR**  
**DR. DONALD J. PINKAVA**  
**AUGUST 29, 1933–JULY 25, 2017**

A little over a year ago we lost our colleague and friend, Don Pinkava. We all have good memories of our time together. Don was a passionate scientist, editor, collector of plants (and many other things), and a generously supportive colleague. One of his most significant contributions has been his mentoring of students. The following accounts have been written by four of his students, David Keil, Wendy Hodgson, Marc Baker, and Dixie Damrel. They span his long teaching career at Arizona State University and provide a little insight into life at the Arizona State University Herbarium over the years. These are only a few of the many students and colleagues that were influenced by Don's gentle mentoring.

DAVID J. KEIL

As a sophomore at ASU in 1966 I enrolled in Arizona Flora, a class taught by a young botany professor named Don Pinkava. It was an oddly structured class with only one lecture per week but lots of lab time, plus some field trips. Dr. Pinkava introduced us to some basic botanical terminology and then took the class out on campus to learn keying skills by keying out campus trees. I quickly caught on, as I already knew how to use a key, and my high-school Latin helped me to learn the terms. When Dr. Pinkava introduced us in lab to flowers, he could tell that I was interested. In our first keying lab he introduced Kearney & Peebles's Arizona Flora. That day I discovered the fun of solving botanical puzzles.

In subsequent labs Dr. Pinkava introduced the herbarium and taught us how to use a plant press. I was hooked. I began collecting plants on class trips and bicycled into the desert to collect on my own. Dr. Pinkava encouraged me as my interest deepened, and he and Elinor Lehto, Curator of the ASU herbarium, invited me to go on a field trip with them to Lake Pleasant Regional Park. On April 6, 1966 a ranger took us in a motorboat to an isolated area where we spent hours hiking about, discovering, collecting, learning, and enjoying each other's company. Thus began shared field adventures that lasted for years. By the semester's end I was becoming a taxonomist, and I asked Dr. Pinkava to be my advisor.

That summer I returned to my parents' home in the Chicago area, purchased a copy of the Illinois Flora, made my own plant press, and proceeded to collect and learn the plants I'd grown up with. I discovered that the skills and knowledge of plant families I'd acquired in Arizona were transferable. I returned to ASU that fall with boxes of plants. Dr. Pinkava and Elinor helped me with the botanical challenges, pointed me to references that I could use, and gave me access to the herbarium. And a work-study job as an herbarium assistant!



In spring 1967 the desert exploded in bloom. I took a collecting trip on my own along the Apache Trail, brought back bags of plants, and Dr. Pinkava, Elinor, and I spent much of the following week processing my gatherings, which included several plants not represented in the ASU herbarium. Dr. Pinkava invited me along on the Arizona Flora class trips, and to my great surprise, he divided the class into three groups. He took one group of students, Elinor led a second group, and he assigned a third group to me. It was a huge vote of confidence for me from my mentor.

In 1967 Dr. Pinkava received a grant to support research on the Arizona Flora and to increase the holdings of the herbarium. He and Elinor and I would pile into his Mustang and head out to some remote area of the state where we tried to collect every plant we encountered. We collected all day, and if it was an overnigher, pressed plants by lantern light, sometimes until midnight or later. The banter in the car, in the field, around the picnic table, and later in the herbarium was that of friends and of a mentor guiding his students. Dr. Pinkava was strict on some aspects of our relationship—if we stopped for a restaurant meal, he *always* picked up the tab.

I took several classes from Dr. Pinkava, and enjoyed them all. I learned much from what he taught, *and* from how he taught. He respected his students. He listened. He encouraged. It was clear from his classes and from the time he spent outside class preparing that he invested himself in his students. When I served as his lab assistant, he guided me. Sometimes it involved letting me make mistakes, and then helping me to learn through them. He knew when to let me take the initiative and when to reel me in. Dr. Pinkava was my role model as a teacher.

I graduated in 1968 and continued on for a master's degree. Right after graduation Dr. Pinkava, Elinor, and I traveled to Cuatro Cienegas, in Coahuila, Mexico, where he was investigating the flora. The trip over was eventful, with a car breakdown in New Mexico, the most spectacular thunderstorms I've ever experienced, and our arrival punctuated by a pounding hailstorm. What followed was a time of exploration, my first experience in another culture, exposure to a new flora, a backpack climb into a desert mountain range, and wonderful memories. Dr. Pinkava was always true to his Catholic faith; even in this remote area of Mexico, he sought out the local church and attended Sunday mass.

My master's degree project was a study of the vegetation and flora of the White Tank Mountains. Dr. Pinkava took on a new mentoring role for me as I attempted to write my thesis. Time after time he chopped, questioned, edited, and rewrote, as he helped me to transform my raw prose into something that I could be proud of. I have no idea how much time he poured into my writing, but I am forever grateful to him. I am a far better writer and editor because of his critical editorial attention.

I completed my master's in 1970 and entered the U.S. Army as a second lieutenant. My plans for further education were on hold as I looked at two years of active duty, including a likely stint in Viet Nam. Six weeks into my officer training my cohort of young officers was offered an early exit—the Army had discovered they had too many junior officers. That night I called Dr. Pinkava

with the news and asked for advice on applying to a Ph.D. program. He came up with several suggestions, and soon I was admitted to Ohio State.

Because of Dr. Pinkava's tutelage I was well prepared to start my research. He had taught me how to dig into literature and how to write good scientific prose. I jumped into my research. Soon after arriving at Ohio State I wrote a grant proposal that led to NSF support, and by summer 1971 to an extensive field trip in Mexico, accompanied in the first half by Lyle McGill, another of Dr. Pinkava's protégés. Thanks to my preparation under Dr. Pinkava, I had field and lab skills that I was ready to use.

I received my Ph.D. in June of 1973. Over the next two years this was followed by a succession of short-term teaching and research positions, none of which led to permanent employment. In August 1975, without a job and in the hope of getting leads on employment opportunities, I attended the AIBS (American Institute of Biological Sciences) national meeting at Oregon State. There I ran into Malcolm McLeod, another of Dr. Pinkava's former grad students. Malcolm had a teaching position at California Polytechnic State University. We reminisced about times at ASU, and when Malcolm learned I was looking for a job, he suggested that I stop for a visit—there might be an opening at Cal Poly. I did visit, but no job materialized then. I continued on to Phoenix, where my parents now lived.

I drove over to ASU and visited Dr. Pinkava. We compared notes. He was trying to get a promotion to Professor. I needed a job. We both reckoned that research publications would enhance our chances of achieving those goals. So Dr. Pinkava made space for me in his lab, and we undertook research projects that led to a series of papers. It was a productive year, with personal and professional growth, and I experienced Dr. Pinkava's mentorship at a new level. In the end he was promoted, and I got my job. Malcolm let me know that a position had opened up at Cal Poly, and I began my 40+ year career there.

Over the years I made frequent visits to ASU. I'm not sure just when he became Don to me and not Dr. Pinkava—we were colleagues for many years. I spent a sabbatical at ASU in 1989. I always felt comfortable when we talked. He was a humble man, a good man, and a true gentleman. My visits became less frequent after my kids came along, but Don was always in my heart. The party for Don's 80<sup>th</sup> birthday was the last time I saw him. I am honored to have had him as my mentor, colleague, and friend.

David J. Keil. Ph.D.  
Professor Emeritus  
Biological Sciences Department  
California Polytechnic State University



WENDY HODGSON

Dear Dr. Pinkava,

I remember the day we first met, back in the spring of 1972—over 45 years ago. You were wearing that tan dress jacket, the only one that I think you had until you met Mary. That Arizona Flora class changed my life. Your enthusiasm and passion was infectious—I spent 4 days a week in your lab trying to key out those plants. I loved our field trips, all of us frantically writing down scientific names as you effortlessly announced them to us eager beavers. I, and others I am sure, wondered if some day we too, could ever spout them off like that! That B was the best, most hard-earned B I ever got! I still wanted to study animals, but your encouragement and desire to provide me with numerous opportunities to draw plants altered my direction of career choice. I got my wildlife degree at a time when women were not encouraged—actually, women were discouraged to enter that field. I knew I did not want to pursue this field. *You* encouraged me to pursue botanical illustration and botany in your humorous, non-suspecting but effective manner (and all this coming from someone who was a fine illustrator himself!), sending me on a life course for which I will be forever grateful. I loved drawing plants for you and your students—what an honor for me, especially those plants named in *your* honor (that *Phacelia* will always be my most favorite). Stashing my wildlife degree in a drawer, I excitedly pursued botany under your leadership and mentorship. You provided me the idea of what I might want to do for a thesis—edible plants of the Sonoran Desert, which would include illustrations (and which got me on the path of ethnobotany). During this period, I remember our Garden field trips we took as part of your Arizona Cactus seminar, my old, worn out Benson's Arizona Cacti book in hand. Who knew we and other friends/colleagues you mentored would produce together the beautiful Cactaceae treatment for Intermountain Flora 38 years later? It was project that we would never have been asked to do had it not been for your expertise. Those of us, who were a part of this project, including our illustrious illustrators, will always remember it as the most satisfying and fun project ever worked on. With this under our belt, we started on what seemed a natural transition, updating the Cactaceae of Arizona project, with you leading several of us DBG researchers and outside collaborators. Unbeknownst to you, we had planned to dedicate it in your honor; we will do so as well as dedicate it to you in your memory.

You affected so many people in such a wonderfully positive way, with students following their love of science while developing long-term friendships spanning several decades. How can we forget those fun-filled Christmas gatherings when you, Mary and little Michelle opened your homes to us, celebrating life and good friends, providing opportunities for each of us to express our thoughts, gratefulness and fun stories only eccentric botanists can tell? You always unselfishly shared your ideas, thoughts, and opinions about cacti, agaves, and life, while also listening openly and gamely to our own. All of

us revered your genuine graciousness and respect, as was your love of family and friends.

Every plant we collect, study, describe as new to science, and share with friends/colleagues, will be done so in the spirit of you, gently prodding us on to become better botanists, better persons. Thank you, we love you, Wendy.

Wendy Hodgson  
Herbarium Curator  
Desert Botanical Garden

MARC BAKER

In 1980, I wrote to researchers at several graduate schools in search of a potential major professor. After reviewing my research interests, I was pointed to Dr. Donald Pinkava at ASU as the expert on the Opuntioideae. I wrote to Dr. Pinkava, set up an appointment, and took a bus to Tempe. I did not drive because I was planning to hike around the Sierra Madre Occidental after the interview. I recall the interview very well because I was simply astounded by Dr. Pinkava's intellect. Until that time I was perhaps somewhat full of myself because I had done well on my Biology GREs. The interview with Dr. Pinkava was very humbling, to say the least. At the same time, however, it inspired me to put my nose to the grindstone and learn all I could from this master. Although he was somewhat concerned about my solo hike in the Sierra Madres, he accepted my application, and I started that fall at ASU.

Upon arriving at ASU, I parked my VW bus in an empty field and started classes. After learning of my living arrangement, Dr. Pinkava, in his fatherly manner, demanded that I find more permanent quarters. Throughout my three years as a Ph.D. student, Dr. Pinkava provided wise advice. For example, he suggested I not bother with DNA studies because they were too much trouble for too little data, especially at the population level. He was correct, of course, and only after 30 years have DNA methodologies been developed that provide plenty of data for the dollar. Of course, someone had to develop those methods, but it was not my aim to do so.

Dr. Pinkava's knowledge of the Opuntioideae, as well as other cacti and the flora of Arizona, was immense. This was not only because he was smart but also because he was diligent. Early every morning, he was reading, organizing, and requesting reprints. He was also assiduous with his teaching and, although he demanded much from his students, he was loved by them. After graduating from ASU and taking several detours, I have spent much of the intervening 30 years interacting with Dr. Pinkava, all of which has been positive and academically exciting. With every discovery in the field, no matter how small, it was Dr. Pinkava whom I would call, and I can still hear his gentle voice of

encouragement. He was my academic father, as well as for many successful students. He was one of those rare individuals who lived a virtuous, productive, and exemplary life.

Marc Baker  
Consulting Botanist  
Adjunct Professor  
Arizona State University

DIXIE Z. DAMREL

I came to know Dr. Pinkava in his later teaching career and unexpectedly ended up being one of his last graduate students. I'd first returned to university life after a separate and unrelated career, thinking that I wanted to study horticulture. But all it took was time volunteering in the Herbarium—and a semester of Dr. Pinkava's legendary Plant Taxonomy class—to put me on an entirely different path.

It was as an ASU herbarium volunteer, gluing labels on genus covers in the Cactaceae collection (and coming to accept the natural infusion of glochids secondary to the work) that I briefly first met Dr. Pinkava. He was a quiet background presence and ever busy professor who would regularly spirit into the cactus collection mentoring other botanists and was always, always reviewing specimens.

Other students spoke in reverential tones about Dr. Pinkava and insisted that if you hadn't taken the Pinkava Plant Tax class, then you really hadn't taken the ultimate journey! For so many, this course was an eye-opening rite of passage where you learned to really *see* a plant instead of simply look at it. Dr. Pinkava's lectures were amazing revelations delivered in his calm, direct and demanding manner. He taught labs by the "old school" method, with students drawing, coloring, labeling, dissecting; struggling to relate the terminology to the actual structure under the scope, and wondering how many terms for hair-like "trichomes" a person needed to know. The convoluted couplets of the dichotomous key were lessons in humility. Yet, Dr. Pinkava conducted the class like a patient Old World Santa Claus. He would bring wonderful gifts but the recipient would have to practice and work hard to identify every feature of each gift. By the end of the course, recognizing the features of a plant became an unconscious reflex. Indeed, it became hard to remember that there was a time when one looked at a plant and did not actually "see" it.

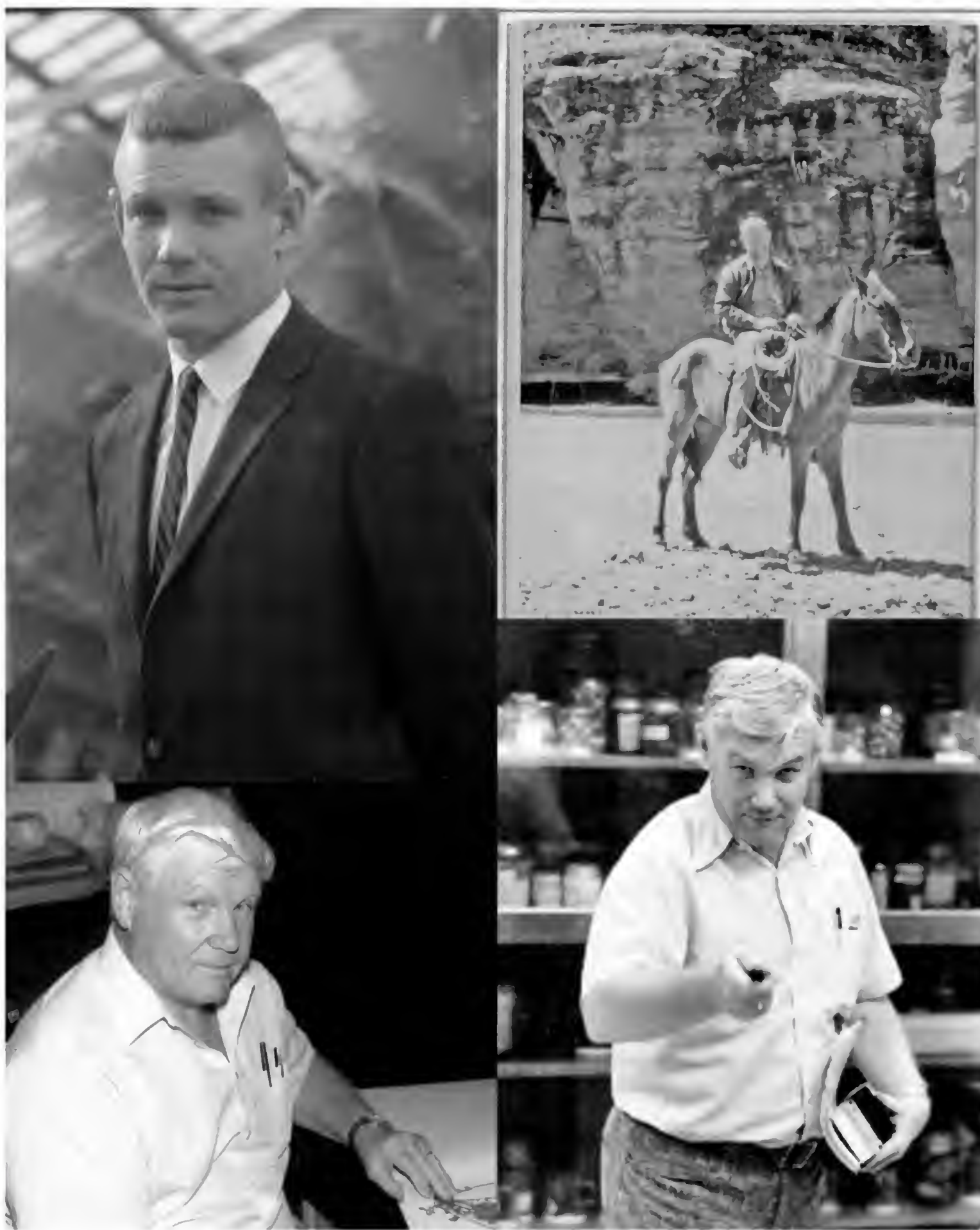
As a graduate student I had the life-changing opportunity to work with Dr. Pinkava as a research assistant on "The Phoenix Flora," a project that reviewed herbarium specimens at Arizona State (ASU) and at the Desert Botanical Garden (DES). Working side by side, Dr. Pinkava and I went through all of the Arizona specimens in both herbaria. What a privilege to receive an extraordinary and personalized tour of Arizona flora, conducted by a patient master who treated me (as he did all his graduate students) as a genuine colleague. As Dr. Pinkava



would discuss the specimens and taxa, I tried to imprint each one in my mind and memorize his comments about the plants and his stories—true botany lore—about collecting and collectors. When we came across a specimen with an identification I thought questionable, he encouraged me to speak up about it, no matter who had collected it. Correct data were important to him. When he noticed that one portion of the Phoenix region was under-collected, the area southeast of Phoenix, he encouraged me to do a floristic study of the San Tan Mountains Regional Park to remedy that situation.

One of the great treasures of this wonderful time in the herbarium was seeing the kindness and camaraderie that Dr. Pinkava offered his students. We broke for lunch every day at Dr. Pinkava's insistence, and in this informal setting he gave us a sense of belonging and confidence, and encouraged (some might say challenged) us to find our voices as professional botanists. His delight in being a botanist was contagious, as were his enthusiasm and charming, sly sense of humor. I think these were very important gifts. One could see his joy whenever one of his students came in with a press full of plants. Although he had been a botanist for many, many years, Dr. Pinkava was always happy and eager to sit down with the student to see what was in the press—for him, it was like opening a treasure chest. His enthusiasm made his students feel that their work was genuinely important, and his high standards made them feel prepared and inspired to undertake meaningful lives in botany.

Dixie Z. Damrel  
Curator  
Clemson University Herbarium



**Figure 1.** Photos of Don Pinkava over the years. Clockwise from upper left. Probably as a student at Ohio State University mid 1950s to mid 1960s. Don on fieldtrip to Mexico in late 1960s or early 1970s. Professor Pinkava 1980s. Don near retirement 1990s.





**Figure 2.** Photos of Don Pinkava over the years. Clockwise from upper left. Just home from trip to Mexico (with a beard) in about 1977. On a family trip in about 1974. At 80th birthday celebration. Front row: Tim Reeves, Don Pinkava, David Keil. Middle row: Liz Slawson, Wendy Hodgson, Kathy Rice, Cindy Zisner, Linda Reeves, Raul Puente. Back row: John Anderson, Lyle McGill, Steffi Ekert Bond, Marc Baker, Jon Rebman, Andrew Salywon, Greg Imdorf, Shannon Doan, Kathleen Pigg, Liz Makings, Les Landrum, Marty Wojciechowski.



## ALISMATACEAE

## WATERPLANTAIN OR ARROWHEAD FAMILY

Jon M. Ricketson  
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Terrestrial to submerged annual or perennial herbs, usually erect and scapose, monoecious or bisexual, mostly glabrous to stellate pubescent, bearing lactifers in most organs; sap milky. ROOTS fibrous. STEMS cormose, rhizomatous, or stoloniferous, the rhizomes often terminated by tubers. LEAVES basal, submerged, floating or emergent, sessile or petiolate, with a sheathing base, non-auriculate; blades linear, to hastate, with or without pellucid markings of dots or lines; margins entire or undulate; venation reticulate, the primary veins parallel from base of blade to apex, the secondary veins reticulate. INFLORESCENCE scapose, usually erect, rarely floating or decumbent, racemose or paniculate, rarely umbellate, bracteolate. FLOWERS bisexual or occasionally unisexual, hypogynous, subsessile to long pedicellate; perianth imbricate or involute in bud, actinomorphic; sepals 3, usually green, persistent; petals 3, deciduous; stamens 0 to many, free; filaments filiform or dilate flattened; anthers 2-loculed, elongate, basifixed or versatile, dehiscing by longitudinal slits; pistils 0 to many, superior, free or joined at the base, whorled in a ring or spirally arranged on the receptacle; style terminal or lateral, usually persistent; stigma linear; ovary unilocular, ovules 1 or rarely 2; placentation basal. FRUITS achenes or follicles, compressed or terete. SEEDS 1 to few, U-shaped.—12 genera, ca. 80 spp., nearly worldwide. Haynes & Holm-Nielsen (1994); Haynes & Hellquist (2000); Reveal (1977).

Eight species of Alismataceae are known from Arizona, however only three are commonly collected (*Alisma triviale* Pursh; *Sagittaria cuneata* E. Sheld.; *Sagittaria longiloba* J. G. Sm.); three are rarely found (*A. gramineum* Lej.; *Echinodorus berteroi* (Spreng.) Fassett; *Sagittaria montevidensis* Cham. & Schltdl. subsp. *calycina* (Engelm.) Bogin) and the final two taxa (*S. graminea* Michx. subsp. *graminea*; *S. latifolia* Willd.) have not been recollected in over 100 years.

1. Pistils arranged in a single flattened, circular or triangular whorl; receptacle small, flat; stamens 6. .... *Alisma*
- 1' Pistils spirally arranged, densely crowded over the entire surface of the large globose receptacle; stamens more than 6.
2. Flowers all bisexual; fruiting head bur-like; achenes terete, mostly ribbed with glands between the ribs; leaves with rounded or subcordate bases; stems and petioles angled. .... *Echinodorus*
- 2' Flowers, at least the proximal, unisexual; fruiting head smooth, not bur-like; achenes flattened, often with curved wings and one or two glands; leaves with sagittate to hastate or tapering bases; stems and petioles smooth or terete.....  
..... *Sagittaria*

**Alisma L.** Waterplantain, Mudplantain

Perennial herbs, emersed or along the margins of wet areas, glabrous. STEMS erect, rhizomes often present. LEAVES sessile or petiolate; blades highly variable in shape and size, even within species; linear to elliptic or lanceolate to ovate, apically acute to rounded; bases attenuate to rounded; margins entire; midvein conspicuous, the lateral veins usually 2 to several usually conspicuous. INFLORESCENCE paniculate, often large and open, often bearing hundreds of flowers, erect or emersed, rarely submersed (usually only due to flooding), inflorescence and floral bracts present. FLOWERS bisexual, pedicellate; floral bracts present; receptacle flattened; sepals erect, green; petals white, rarely pink or purplish, entire or slightly erose, generally larger than the sepals; stamen 6–9, the filaments filiform; pistils distinct, 5–20, in a circular or triangular whorl on a flattened receptacle; style lateral; ovules 1. FRUITS laterally compressed achenes, often with 1 or 2 grooves on the curved back, the beak usually persistent, short, straight or curved.  $x = 7$ .—9 species; nearly worldwide, but mostly temperate. (Greek: *alisma*, an ancient aquatic plant, adopted by Linnaeus from Dioscorides). Haynes & Hellquist (2000).

The species are extremely difficult to identify without mature fruits.

1. Fruits with 2 grooves on the back of the achene; leaf blades 3–9 times as long as wide; inflorescence generally much shorter to slightly longer than the leaves..... *A. gramineum*
- 1' Fruits usually with 1(–2) groove(s) on the back of the achene (sometimes smooth); leaf blades 2–4 times as long as wide; inflorescence generally much longer or slightly longer than the leaves. ....*A. triviale*

**Alisma gramineum** Lej. (grassy, grass-like). Grassleaved Waterplantain; Grasslike Waterplantain; Lanceleaf Waterplantain; Narrowleaf Waterplantain; Geyer Waterplantain.—Submerged or amphibious perennial herbs, 0.5–50 cm tall. STEM generally erect (except when submerged), usually 0.3–4 cm in diam. LEAVES basal, usually erect, often floating; submersed leaves sessile, ribbon-like; floating leaves linear, 15–100 cm long, 0.2–3 cm wide; emergent leaves usually petiolate, 5–6 cm long, 0.4–1.5 cm wide, 3–5-veined, usually much longer than the inflorescence, linear-lanceolate or lanceolate to narrowly elliptic, apically acuminate to acute, the base attenuate; petiole sheathing, 5–15 cm long. INFLORESCENCE 15–50 cm long, usually erect, usually shorter than leaves, narrowly verticillate paniculate, the rachis branches in 2–5 whorls, each with 3–5 shortened main branches terminating abruptly in umbellate cymes; pedicels stout, 0.5–4.5 cm long, often recurved in fruit. FLOWERS 4–8 mm in diam.; sepals greenish, 1.5–3 mm long, ovate, not obviously gibbous, apically acute to obtuse; petals white, becoming pinkish tinged, 2–4 mm long, obovate to rounded, apically obtuse, the margin entire to slightly erose; stamens 6–9, 1.4–2.5 mm long; filaments 1–2 mm long nearly as wide as long; anthers 0.3–0.6 mm long, ovoid; pistils 5–20, arranged in an obscurely triangulate whorl, the styles lateral, curved, 0.4–0.5 mm long. FRUITS 5–20, achenes, 2–2.7 mm long, orbicular to orbicular-cuneate, with 2 grooves on the curved back, the central ridge raised above the lateral ridges, the beak often becoming curled.  $2n = 14, 16$ . [*A. geyeri* var. *angustissimum* (DC.) Lunell; *A. gramineum* var. *angustissimum* (DC.). Hendricks; *A.*



*plantago* var. *angustissimum* DC.; *A. gramineum*, C. C. Gmel.; *A. geyeri* Nicolle; *A. gramineum* var. *geyeri* (Nicollet) G. Samuels].—Completely submerged or in mud of marshy areas and lakes: Apache Co. (not confirmed), Coconino Co. (Lake Mary and Marshall Lake); 2,050–2,150 m (6,800–7,100 ft); fl. May–Sep (fr. Sep–Oct); n temperate N. Amer. and Eurasia.

***Alisma triviale*** Pursh (commonplace, ordinary). Northern Waterplantain—Terrestrial perennial herbs to 1 m tall. STEM erect, 1–4 cm in diam. LEAVES basal, erect, emersed, (rarely submerged or floating during flooding), 5–35 cm long, 3–12 cm wide, 5–7-veined, usually much shorter than the inflorescence, linear-lanceolate or elliptic to ovate, apically sub-obtuse to acute or acuminate, basally cuneate to rounded or subcordate; petiole sheathing, 3–20 cm long. INFLORESCENCE simple or compound, a narrow or sub-spherical panicle, to 1 m tall, to 70 cm in diam., usually much taller than the leaves, with 3–9 whorls, each with 3–6 main branches (these can be much branched), gradually terminating in umbellate cymes; pedicels ascending or erect, 0.5–4 cm long, usually erect in fruit. FLOWERS 7–12 mm in diam.; sepals green, 3–6 mm long, ovate to suborbicular, somewhat gibbous in most, apically acute; petals white becoming purplish tinged, rhombic, 3.5–6 mm long, apically obtuse, the margins entire to slightly erose; stamens 6–9, 2.6–4 mm long; filaments 2–3 mm long, slender; anthers 0.6–1 mm long, ovoid; pistils 5–20, arranged in an obscurely triangulate whorl; styles lateral, straight or slightly curved, 0.4–0.7 mm long. FRUITS 5–20, achenes, 2.1–3 mm long, ovoid, with 1 or 2 grooves (these sometimes shallow), on the curved back, sometimes smooth, often variable in the same head.  $2n = 14, 28$ . [*Alisma plantago* var. *triviale* (Pursh) Britton, Sterns & Poggenb.; *A. plantago-aquatica* L. var. *americana* Schult. & Schult. f.; *A. plantago-aquatica* L. var. *triviale* (Pursh) Farw.].—In and along the margins of freshwater lakes, ponds, tanks and streams, rarely in deep water: Apache, Coconino, Graham, Navajo and Yavapai cos.; 1,050–2,600 m (3,400–8,500 ft); fl. May–Sep, (fr. Aug–Oct); N. Amer.

Some confusion has occurred in the Arizona flora over the years regarding the true identity of the most common *Alisma* in the state. It is believed now that the name *A. plantago-aquatica* L. refers to a primarily Eurasian species and our material should be referred to as *A. triviale* Pursh (Haynes and Hellquist, 2000: 25).

### **Echinodorus** Rich.

Burhead

Annual or perennial herbs, bisexual, emersed, floating-leaved or rarely submersed, glabrous to stellate pubescent. STEMS with rhizomes present or absent. LEAVES sessile or petiolate; linear to lanceolate to broadly ovate, apically obtuse to acute or acuminate, basally attenuate to cordate, the margins entire or undulating with pellucid markings absent or present as dots or lines; petiole mostly triangular, rarely terete, sheathing at base. INFLORESCENCES erect, racemes, panicles or rarely umbelliform; rachis branches in whorls of 1–18, erect or rarely decumbent; bracts, glabrous, often papillose along the veins. FLOWERS bisexual, subsessile to pedicellate; pedicels often elongating after anthesis, ascending to recurved; sepals persistent, membranaceous coriaceous, reflexed to spreading; petals white, deciduous, larger than sepals, the margins entire; stamens 9–25; filaments linear, glabrous;



anthers versatile or basifixed; pistils distinct, 9 (–250 or more), spirally arranged on convex receptacle, forming a head; style terminal or lateral, persistent; ovule 1 per pistil. FRUITS achenes usually terete, often longitudinally costate, the beak terminal or lateral. [*Helianthium* J. G. Sm.; *Albidella* Pichon].—40–50 spp., native to the New World, but spreading to Eur., Afr. and Asia. (Greek: *echinus* = rough husk + *doros* = leather bottle, referring to the fruit). Haynes & Holm-Nielsen (1994); Haynes & Hellquist (2000).

***Echinodorus berteroi*** (Spreng.) Fassett (for Carlo Giuseppe Bertero, 1789–1831, an Italian physician). Bertero Burhead.—Annual or perennial herbs, to 70 cm tall; glabrous. STEMS rhizomatous. LEAVES petiolate, submerged or emerged; submerged leaves rare, generally narrower; emerged leaves elliptic, lanceolate to ovate, 2.6–15.5 cm long, 0.5–20 cm wide, apically obtuse to acute; base truncate or occasionally cordate to broadly rounded to tapering; margins entire midvein prominent, the secondary veins 3–11, usually prominent; petioles terete to triangular, 2–36 cm long, 1–15 mm in diam., with a basal sheath. INFLORESCENCE racemose, rarely paniculate, erect, 1.5–40 cm long, 1.7–50 cm wide, usually much taller than the leaves, 1–9 whorls, each whorl 1–4-flowered, the rachis triangular; peduncles angled, 3–5-ridged; pedicels spreading to ascending in flower and fruit, cylindrical, 6–28 mm long, 0.4–0.6 mm wide. FLOWERS 6–11 mm in diam.; sepals broadly triangular, 0.9–3.4 mm long, 1.3–2.9 mm wide, spreading to reflexed, with 9–13 veins; petals white to cream or greenish-white, rhombic to orbicular, 2.5–4.8 mm long, 3.5–4.5 mm wide, spreading, clawed, the claw to 0.5 mm long; stamens 9–15; filaments slender, to 7 mm long; anthers versatile, to 8 mm long, apically obtuse; pistils 45–200; styles straight. FRUIT oblanceolate, terete, 0.9–3.2 mm long, 0.6–2.5 mm wide, 3–5-ribbed, the beak terminal, erect, 0.6–1.3 mm long.  $2n = 22$ . [*Alisma berteroi* Spreng. (as "berterii"); *A. rostratum* Nutt.; *Echinodorus rostratus* (Nutt.) A. Gray].—Streams, ditches, and marshes: Yuma Co., around Yuma, n of Imperial Dam, along the Colorado R.; to 150 m (to 400 ft); IL to TX to s CA and s to Mex., the Caribbean, and C. Amer. and S. Amer., incl. Guyana, Venezuela, Ecuador and Peru.

### ***Sagittaria* L.** Arrowhead, Sagittaria

Perennial or rarely annual herbs, monoecious or rarely dioecious, glabrous to sparsely pubescent, submerged, floating-leaved, or emerged. ROOTS fibrous. STEMS often rhizomatous, stoloniferous, or cormiferous, often terminated by tubers, the tubers white to brown, smooth. LEAVES submerged, floating, or emerged, sessile or petiolate, the blades present or absent (submersed leaves often with reduced blades) linear to obovate, apically acute to rounded, basally attenuate, often hastate or sagittate with margins entire, without pellucid markings; petioles terete to triangular. INFLORESCENCE erect or often lax, emerged or floating, racemose, paniculate, or rarely umbelliform, with rachis branches in 1–17 whorls, with 2–3-flowers per whorl; bracts smooth to papillose; flowers staminate above, pistillate below. FLOWERS unisexual, pedicellate, rarely sessile; floral bracts present; pedicels elongating after anthesis, ascending to recurved; receptacle convex. STAMINATE FLOWERS with sepals membranaceous to coriaceous often sculptured, greenish, persistent, usually

reflexed; petals white rarely pink or yellowish, sometimes with a basal purple spot, deciduous, the margins entire; stamens 7–30; filament linear, often dilated, glabrous to pubescent; anthers basifixed, linear to orbicular. PISTILLATE FLOWERS with sepals as in the staminate flowers but erect or reflexed; petals as in the staminate flowers; staminodes sometimes present in lower pistillate flowers; pistils to 1500 or more, distinct, spirally arranged; style terminal; ovule 1 per pistil. FRUITS achenes, numerous, laterally compressed, often laterally ribbed or winged, often with a conspicuous dorsal wing, the beak, usually short erect.  $x = 11$ .—Ca. 30 spp., nearly cosmopolitan. (Latin: *sagitta* = arrow, from the shape of the leaves). Haynes & Holm-Nielsen (1994); Haynes & Hellquist (2000).

1. Pedicels recurved or rarely spreading in fruit; sepals of pistillate flowers usually erect and closely appressed, enclosing the flower or fruiting head; sepals and pedicels generally thickening in fruit. .... *S. montevidensis*
- 1' Pedicels ascending or spreading in fruit; sepals of pistillate flowers spreading or recurved; sepals and pedicels usually not thickening in fruit.
2. Filaments pubescent or minutely scaly, dilated; leaves linear-elliptic to lanceolate, entire, without basal lobes; bracts of the inflorescence thinly membranous, glabrous, more or less connate, with free tips more than 2 mm long. .... *S. graminea*
- 2' Filaments glabrous, linear; leaves typically sagittate, with conspicuous basal lobes; bracts of the inflorescence membranous, glabrous or pubescent, with free tips or connate.
3. Basal leaf lobes as much as 2–3 times longer than the terminal lobe; achene beak short and inconspicuous, mostly erect. .... *S. longiloba*
- 3' Basal leaf lobes shorter or at most subequal to the terminal lobe; achene beak short or long, erect or lateral to retrorse.
4. Terminal leaf lobe sub-equal to slightly longer than the basal lobes; floral bracts united (keeled) or separate, elliptic to lanceolate, 5–10 (–15) mm long, apically rounded to obtuse or broadly acute; achene 2.5–4 mm long, with a conspicuous, lateral, horizontal or retrorse beak, 0.5–1.5 mm long. .... *S. latifolia*
- 4' Terminal leaf lobe longer (often as much as 2 times) than the basal lobes; floral bracts united at least at base, linear to lanceolate, (5–) 10–30 mm long, apically rounded or sharply pointed; achene 2–2.5 mm long, with an often inconspicuous erect or antrorse beak, 0.2–0.4 mm long. .... *S. cuneata*

**Sagittaria cuneata** E. Sheld. (wedge-like). Duck Potato Arrowhead.—Perennial herbs to 110 cm tall, essentially glabrous. STEMS stolons and/or corms. LEAVES submersed, floating and emersed; submersed leaves sessile, linear, phyllodial, 5–45 cm long, 0.5–3 cm wide, 3–7-veined, apically acute; floating leaves petiolate, the petioles triangular, to 100 cm long, with basal sheath, blades cordate or sagittate, rarely linear or ovate, 7.5–9 cm long, 3.5–4 cm wide, 3–9-veined, apically obtuse or acute to acuminate, the basal lobes shorter than the terminal lobe; emersed leaves petiolate, the petioles recurved, triangular, 3.5–51 cm long, 0.5–1 cm wide,



with basal sheath, the blades linear to sagittate, 2.5–17 cm long, 1.5–11 cm wide, the terminal lobe triangular or lanceolate to ovate, often as much as twice as long as the basal lobes, 3–9-veined, apically acute. INFLORESCENCE racemose or rarely paniculate, 14–21 cm long, 2–10 cm wide, rarely branched at the base, usually emersed, the rachis branches in 2–10 whorls, the whorls 3-flowered; peduncles triangular, 10–50 cm long; floral bracts united at least at base, linear to lanceolate, membranaceous, 5–40 mm long, apically rounded to acuminate; pedicels cylindric, ascending in fruit. STAMINATE FLOWERS to 25 mm wide; sepals ovate, recurved to spreading, 4–8 mm long, 3–5 mm wide; petals clawed, 6–10 mm long, 4–5 mm wide, the claws 1–1.5 mm long; stamens 15–24; filaments cylindric, not dilated, 0.8–2 mm long, 0.2–0.3 mm wide, glabrous; anthers linear, 1–2 mm long, 0.5–0.8 mm wide, apically obtuse; with pistillodes. PISTILLATE FLOWERS as in the staminate flowers; sepals not enclosing the flower or fruiting head, 10–15 mm long, 8–10 mm wide; petal clawed, 15–20 mm long, 1–15 mm wide, the claw 0.5–0.8 mm long; staminodes absent. FRUITING HEADS 8–15 mm in diam. FRUITS obovoid 1.8–2.5 mm long, 1.3–2.5 mm wide, the beak 0.2–0.4 mm long, usually keeled, usually without wings.  $2n = 22$ .—Lakes, ponds, tanks, marshy areas and rivers: Apache, Coconino, Navajo, Pinal cos.; 1800–2150 m (6000–7100 ft); fl. Jun–Sep (fr. Jun–Oct); throughout N. Amer., except the se.

**Sagittaria graminea** Michx. (grass-like). Grassy Arrowhead.—Annual or perennial herbs to 100 cm tall. STEMS rhizomatous. LEAVES submerged and/or emersed; submerged leaves sessile, linear, phyllodial, 6.4–10 cm long, 0.5–4 cm wide, 3–7-veined apically acute, the basal lobes absent; emersed leaves petiolate, the petioles triangular, 6.5–13.5 cm long, 0.7–1.2 cm wide, with basal sheath; blades linear to linear-oblongate, 2.5–17.4 cm long, 0.2–4 cm wide, 1–3-veined, apically acute, the basal lobes absent. INFLORESCENCE racemose or paniculate, emersed, 2.5–21 cm long, 1–6 cm wide, often branched at the base, the rachis branches in 1–12-whorls, the whorls 3-flowered; peduncles terete, 6.5–29.7 cm long, 0.2–4 cm wide; floral bracts united, broadly subulate to lanceolate, chartaceous, 2–5 cm long, apically acute to obtuse; pedicels cylindrical, spreading in flower and fruit. STAMINATE FLOWERS to 2.3 cm wide; sepals reflexed to spreading, 3–4 mm long, 2–2.5 mm wide; petals without claws, 5–8.5 mm long, 4–5 mm wide; stamens 12–18; filaments cylindric and dilated, 0.1–0.5 mm long, 0.05–0.2 mm wide, shorter than the anthers, pubescent; anthers elliptic, 0.9–1.1 mm long, 0.6–1 mm wide, apically obtuse; pistillodes absent. PISTILLATE FLOWERS as in the staminate flowers; sepals not enclosing the flowers or fruiting head, 3–5 mm long, 1.5–2.5 mm wide; petals 6–8 mm long, 5.7–6.3 mm wide; staminodes absent. FRUITING HEADS 6–10 mm in diam. FRUITS oblongate, 1.5–2.8 mm long, 1.1–1.5 mm wide, the beak 0.1–0.4 mm long or obsolete, without faces etuberculate.  $2n = 22$ .—3 subspp., throughout N. Amer., scattered in the W. Ind.

Subsp. **graminea**. —LEAVES submersed to less than 1 cm wide. INFLORESCENCE racemose; bracts moderately connate, the tips up to 6 mm long. FLOWERS with filaments equal or shorter than the anthers; pistillate flowers pedicellate and ascending, 0.5–3 cm long. [*Sagittaria angustifolia* Lindl.].—Marshy areas: Graham Co.; known from a single collection, *J. Thornber s.n.*; ca. 1350 m



(4400 ft). Throughout most of N. Amer.

**Sagittaria latifolia** Willd. (broad-leaved). Common Arrowhead, Wapato, Duckpotato.—Perennial herbs to 45 cm tall, glabrous (ours) or pubescent. STEMS stolon and/or corms. LEAVES emersed, petiolate, the petioles erect or ascending, triangular, 6.5–51 cm long, 0.2–0.8 cm wide, with basal sheath, the blades sagittate or rarely hastate, 1.5–30.5 cm long, 2–17 cm wide, 7–13-veined, the terminal and basal lobes essentially equal, or the terminal slightly longer, apically acute or rarely obtuse. INFLORESCENCE a simple raceme or rarely paniculate, emersed, 4.5–28.5 cm long, 4–23 cm wide, rarely branched at the base, the rachis branches in 3–9-whorls, the whorls 3-flowered; peduncles triangular, 10–59 cm long, 0.05–0.07 cm wide; floral bracts united (keeled) or separate, elliptic to lanceolate, membranaceous, 3–8 mm long, apically obtuse; pedicels cylindric, spreading. STAMINATE FLOWERS to 4 cm wide; sepals reflexed to spreading, 5–6 mm long, 3–4.5 mm wide; petals clawed, 6–9 mm long, 4.5–5 mm wide, the claws ca. 1.5 mm long; stamens 16–18; filaments cylindric, not dilated, 1–3 mm long, 0.2–0.3 mm wide, longer than the anthers, glabrous; anthers linear, 1.2–1.9 mm long, 0.5–0.6 mm wide, apically obtuse; without pistillodes. PISTILLATE FLOWERS as in the staminate flowers; sepals reflexed not enclosing the lower or fruiting head, to 10 mm long, to 8 mm wide; petals clawed, to 18 mm long, to 12 mm wide, the claw to 0.5 mm long. FRUITING HEADS 10–17 mm in diam. FRUITS oblanceolate, 2.5–3.5 mm long, to 2 mm wide, the beak 1–2 mm long, without keel, the faces etuberculate.  $2n = 22$ .—Streams: Pima Co.; ca. 750 m (2500 ft); widespread in the New World. Known from only three J. Thornber collections between 1903 and 1905 from the Rillito R., near Fort Lowell [Tucson].

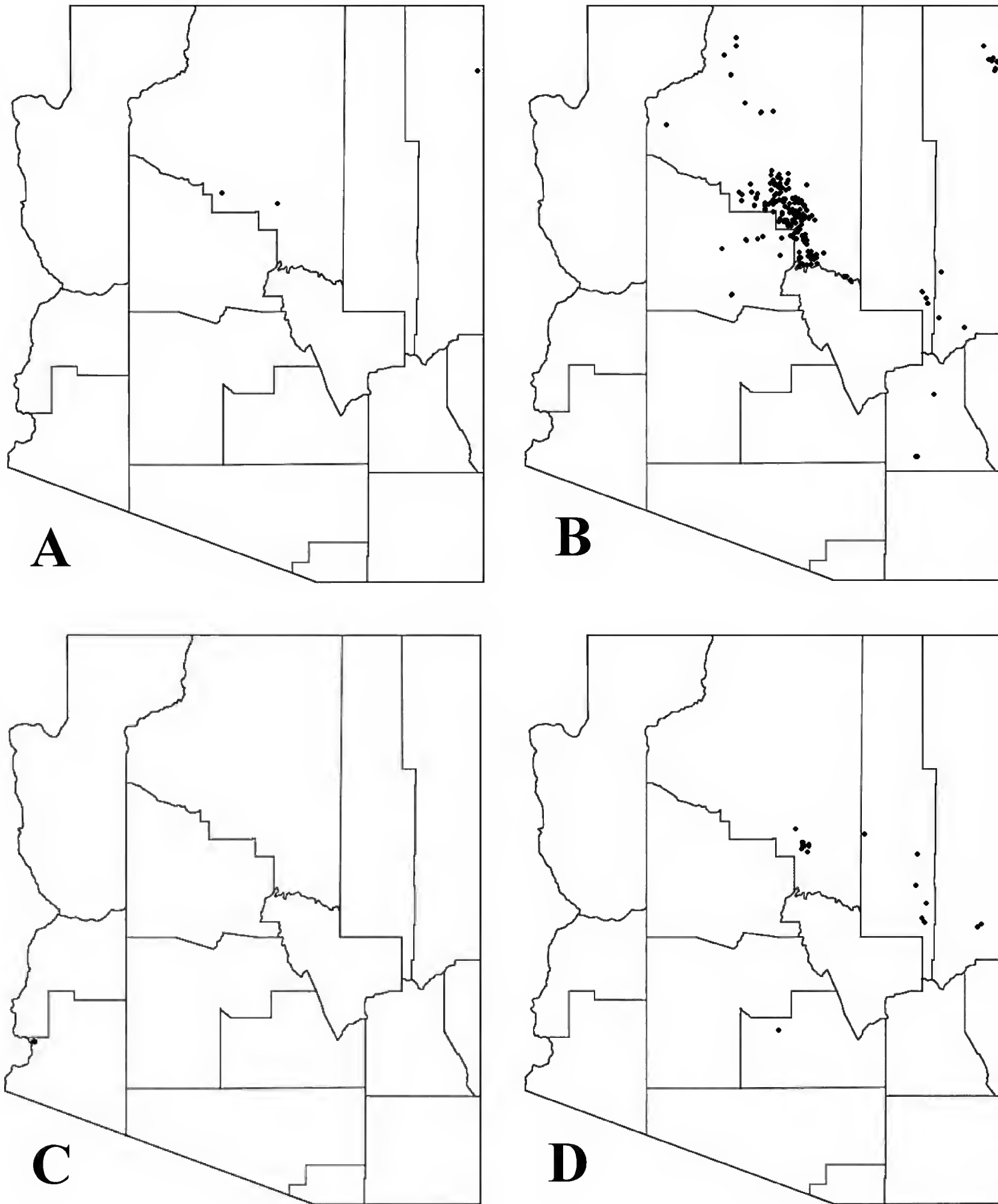
**Sagittaria longiloba** J. G. Sm. (long lobes, of the leaves). Longbarb Arrowhead.—Perennial herbs to 100 cm tall, essentially glabrous. STEMS stolons and/or corms. LEAVES emersed, petiolate, the petioles erect, flattened, 5-angled, 24.5–60 cm long, 0.2–8 mm wide, with basal sheath, the blades sagittate, 11.5–26.5 cm long, 0.8–15 cm wide, 5–15-veined, the basal lobes always longer, commonly twice as long as the terminal lobe, apically acute to obtuse. INFLORESCENCE a simple raceme or rarely paniculate, emersed, 20–37 cm long, 5–27 cm wide, the rachis branches in 5–7 whorls, the whorls 3-flowered; peduncles terete, 25–96 cm long, 0.2–7.5 mm wide; bracts united at least at base, lanceolate, membranaceous, 1–15 mm long, apically acute; pedicels spreading. STAMINATE FLOWERS to 30 cm wide; sepals reflexed to spreading, 5–9 mm long, 3–6 mm wide; petals clawed, 5–12 mm long, 3.7–14 mm wide, the claws 1.4–3 mm long; stamens 12–16; filaments cylindric, not dilated, 1–3 mm long, to 0.1 mm wide, glabrous; anthers linear, 1.5–2.2 mm long, 0.3–1 mm wide, apically obtuse; pistillodes absent. PISTILLATE FLOWERS as in the staminate; sepals not enclosing the flower and fruiting head, 5.5–7.5 mm long, 2.4–3.5 mm wide; petals clawed, 6–15 mm long, 4–10 mm wide, the claw ca. 2 mm long; staminodes absent. FRUITING HEADS 4–15 mm in diam. FRUITS oblanceolate, 1.2–2.5 mm long, 0.8–1.6 mm wide, the beak 0.1–0.6 mm long, with keel, the faces tuberculate.  $2n = 22$ .—Ponds, tanks and rivers.: Graham, Pima, and Santa Cruz cos.; 884–1675 m (2900–5500 ft); fl. Apr–Sep (fr. Jun–Oct); mid to w N. Amer, and n Mex.

**Sagittaria montevidensis** Cham. & Schltdl. (from Montevideo, Uruguay). Giant Arrowhead.—Annual or perennial herbs to 100 cm tall. STEMS rhizomes and/or corms. LEAVES submersed and emersed; submersed leaves absent or sessile, linear, phyllodial, to 17 cm long, to 2 cm wide, 1–3-veined, apically rounded to acute, the basal lobes absent; emersed leaves petiolate, the petioles triangular to terete, 21–55 cm long, 0.3–2.5 cm wide, with basal sheath, the blades hastate to sagittate, 2.5–17.5 cm long, 0.6–22 cm wide, 7–20-veined, apically acute, the basal lobes longer than or equal to the terminal lobes. INFLORESCENCE racemose or paniculate, floating or emersed, 1.5–28 cm long, 1.5–15 cm wide, often branched at the base, the rachis branches in 1–15 whorls, the whorls 3-flowered; peduncles terete, 15–47 cm long, 0.2–1.3 cm wide; bracts separate or united, lanceolate to elliptic, membranaceous, 0.4–3.4 cm long, apically obtuse to acute; pedicels cylindric, spreading to erect in flower, reflexed and clavate in fruit. STAMINATE FLOWERS 2–5 cm in diam.; sepals ascending in flower, 7.6–12 mm long, 3–6 mm wide; petals clawed, 10–25 mm long, 5–25 mm wide, the claws ca. 4 mm long; stamens 20–30; filaments cylindric, not dilated, 1.2–7.5 mm, long, 0.3–0.5 mm wide, longer than the anthers, glabrous or weakly pubescent; anthers linear, 1–2.5 mm long, 0.3–1 mm wide, apically obtuse to round-acute; pistillodes present or absent. PISTILLATE FLOWERS as in the staminate flowers; sepals enclosing the fruiting heads, 3.5–12 mm long, 2–9.5 mm wide; petals clawed, 1.25–2.5 mm long, 0.5–3 mm wide, the claw ca. 2 mm long; with or without purple spot at base; staminodes present or absent. FRUITING HEADS 1.2–2.1 cm in diam. FRUIT oblanceolate, 2–4.3 mm long, 0.7–1.5 mm wide, the beak 0.4–0.8 mm long, without keel, faces etuberculate, narrowly winged.  $2n = 22$ .

Subsp. **calycina** (Engelm.) Bogin (calyx).—BRACTS free. INFLORESCENCES with bracts separated. STAMINATE FLOWERS with pistillodes present. PISTILLATE FLOWERS with petals lacking a purple spot at base; staminodes present. [*Sagittaria calycina* Engelm.]—Tanks: Cochise Co.; 1250–1550 m (4100–5100 ft); e N. Amer. and n Mex.

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**Alismataceae.** Figure 1. Distributions: A). *Alisma gramineum*. B). *A. triviale*. (along Colorado River in se AZ) C). *Echinodorus berteroi*. D). *Sagittaria cuneata*.

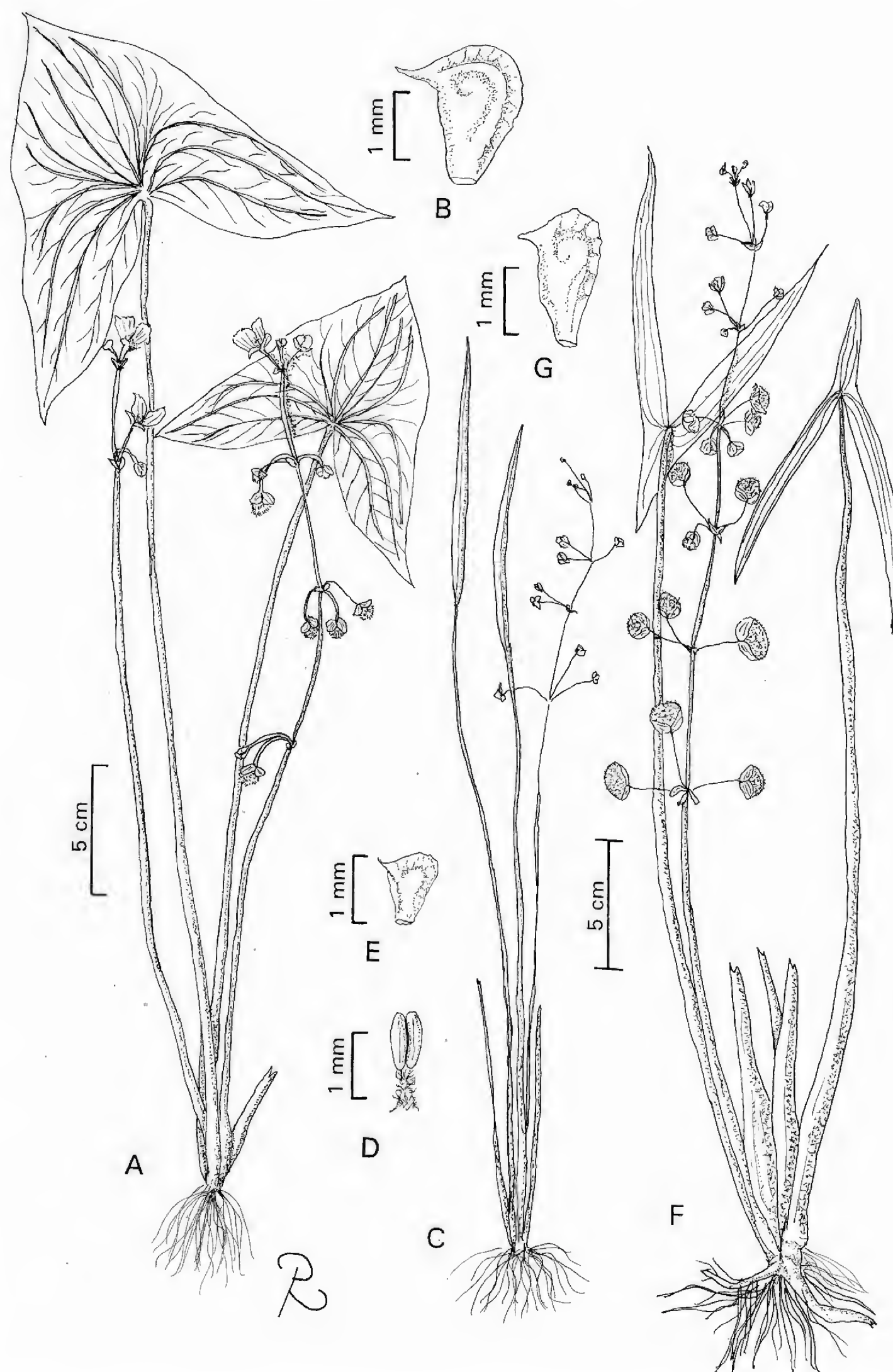




**Alismataceae.** Figure 2. Distributions: A). *Sagittaria graminea* subsp. *graminea*. B). *S. latifolia*. C). *S. longiloba*. D). *S. montevidensis* subsp. *calycina*

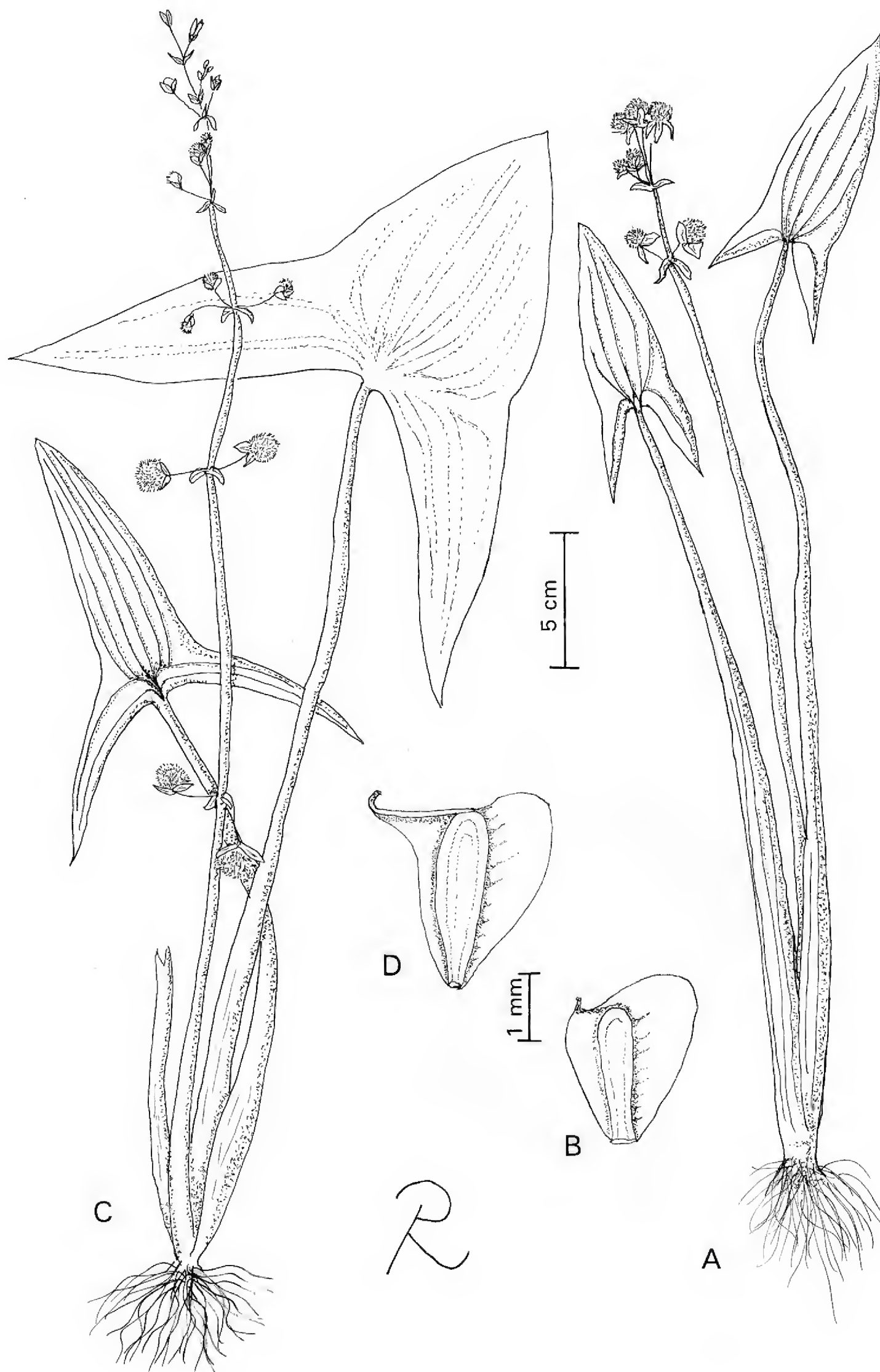


**Alismataceae.** Figure 3. (*Alisma gramineum*; *A. triviale*; *Echinodorus berteroi*). (A–D) *Alisma gramineum*. A) Habit. B) Fruiting head. C) Seed, side view. D) Seed, dorsal view. (E–H) *Alisma triviale*. E) Habit. F) Fruiting head. G) Seed, side view. H) Seed, dorsal view. (I–K) *Echinodorus berteroi*. I) Habit. J) Fruiting head. K) Seed, side view. [Drawn by Jon Ricketson].



**Alismataceae.** Figure 4. (*Sagittaria cuneata*; *S. graminea* subsp. *graminea*; *S. latifolia*). (A–B) *Sagittaria cuneata*. A) Habit. B) Seed, side view. (C–E) *Sagittaria graminea* subsp. *graminea*. C) Habit. D) Stamen. E) Seed, side view. (F–G) *Sagittaria latifolia*. F) Habit. G) Seed, side view. [Drawn by Jon Ricketson].





**Alismataceae.** Figure 5. (*Sagittaria longiloba*; *S. montevidensis* subsp. *calycina*). (A–B) *Sagittaria longiloba*. A) Habit. B) Seed, side view. (C–D) *Sagittaria montevidensis* subsp. *calycina*. C) Habit. D) Seed, side view. [Drawn by Jon Ricketson].

## HYDROCHARITACEAE

## FROG'S BIT FAMILY, TAPE-GRASS FAMILY

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Aquatic annual or perennial, submerged, fresh (ours) and salt water herbs, glabrous or pubescent, monoecious or dioecious or polygamous. ROOTS simple, adventitious, anchored or floating. STEMS cormose, rhizomatous, stoloniferous or erect, simple or branched. LEAVES submerged, rarely floating, basal or cauline and alternate, opposite or whorled, sessile or petiolate; stipules rarely present. INFLORESCENCES axillary, terminal or scapose, 1- to many-flowered, solitary or cymose, sessile or pedunculated, spathate, with 2 wholly or partly connate bracts. FLOWERS usually imperfect, epigynous, actinomorphic or rarely zygomorphic, sessile or born on scape-like peduncles, these usually spirally twisted, the staminate flowers numerous, the pistillate flowers solitary; perianth sessile or on a long slender pedicel-like hypanthium, usually reaching the water surface, the perianth with (2–) 3 tepals per whorl, the tepals free, the outer tepals (1–2 whorls, sepal-like) usually green or white, usually reflexed, valvate, the inner tepals (petal-like) usually showy, sometimes reflexed, imbricate; stamens 0 to many, free, in 1 or more whorls, the inner ones often staminodial; a rudimentary ovary often present in the staminate flowers; staminodes often present on the pistillate flowers; ovary inferior, of 2 to 16 united carpels, unilocular, the placentation parietal, the style terminal, the stigmas 2–15, entire or 2–3-lobed. FRUIT berrylike, sometimes beaked, with the remains of the perianth tube, usually irregularly dehiscent; seeds many, fusiform, ellipsoid, ovoid or spheric, glabrous, papillose or echinate.—17 genera, 76 spp., nearly worldwide. Haynes (2000).

1. Leaves ribbon-like, more than 15 cm long, from a basal rosette; stem shorter than leaves; staminate flowers minute, breaking off before anthesis; inner tepals rudimentary, much smaller than the outer tepals ..... *Vallisneria*
- 1' Leaves not ribbon-like, less than 5 cm long, cauline, opposite or in whorls; stem longer than leaves; staminate flowers larger; inner tepals minute or larger, sometimes showy, usually similar in size and shape to the outer tepals ..... 2
2. Leaf margins sparsely serrulate-denticulate, the tips usually spinose; leaves often with teeth along the dorsal surface of the midrib; tubers present; inner tepals minute, as long as or shorter than the outer tepals; staminate spathe spiny ..... *Hydrilla*
- 2' Leaf margins appearing entire or serrulate to denticulate, with minute single celled teeth; leaves smooth along the dorsal surface of the midrib; tubers lacking; inner tepals larger, showy, as large as or larger than the outer tepals; staminate spathe smooth ..... 3.
3. Middle and upper leaves in whorls of 4 or 6, 1.2–4.0 cm long; staminate spathe 2–4-flowered; inner tepals about 8 mm wide, about 3 times as long as the outer tepals.....  
..... *Egeria*
- 3' Middle and upper leaves opposite or in whorls of 3 (rarely 4 or more), 0.6–1.7 cm long; staminate spathe 1-flowered; inner tepals about 1.5 mm wide or less, similar in size to the outer tepals ..... *Elodea*



**EGERIA** Planch.      South American Elodea

Fresh water perennials, dioecious. STEMS elongate, to 3 m long or more, irregularly branched. LEAVES cauline, scale-like prophylls or elongate foliage leaves; prophylls borne at base of stems and branches, opposite, delicate, the apex acute, the base sessile, transparent to pale green; foliage leaves borne at upper portions of stems and branches, in whorls of 5 or more at each node, flaccid, linear to narrowly oblong, often recurved, the midrib often bearing unicellular spines, the apex sub-obtuse to acute or acuminate, terminating in a single celled spine, the base sessile, the margins appearing entire or serrulate to denticulate, with minute single celled teeth. INFLORESCENCES sessile, with a single flower. FLOWERS unisexual, sessile or on long pedicels (the slender, elongated floral tube or hypanthium pedicel-like), opening above water surface 1(–2) at a time. STAMINATE FLOWERS pedicellate, actinomorphic; outer tepals 3, distinct, green, ovate to suborbicular; inner tepals 3, distinct, shining white, widely elliptic to orbicular, with both surfaces papillose; stamens 9, distinct, the filaments elongate, white or yellow, the anthers basifixed, linear, deep yellow to orange. PISTILLATE FLOWERS with tepals as in the staminate flowers but usually somewhat smaller; staminodia 3, distinct, orange to orange-red, papillose; ovary widely ovoid, 1-locular, the ovules 3–9 the styles 3. FRUIT an ovoid capsule, irregularly dehiscent. SEEDS ellipsoidal or fusiform, mucilaginous.  $2n = 46$ .—2 spp.; worldwide in warmer regions. (Latin: *egeri*, a nymph, in reference to aquatic habitat). Cook & Urmi-König (1984).

**Egeria densa** Planch. (dense, in reference to the density of the leaves along the stems). Waterweed.—STEMS 1–3 mm diam., internodes usually 2.5–24 mm long. FOLIAGE LEAVES usually densely whorled along the stem, 1–4 cm long, 1.5–4.5 mm wide. STAMINATE FLOWERS 2–5 in each spathe; spathes 7.5–12 mm long, 1.2–4 mm wide; pedicels to 8 cm long, 0.6–0.8 mm wide; sepals 2.2–4.4 mm long, 1.1–4 mm wide; inner tepals 4.9–10.5 mm long, 3.3–8 mm wide; filaments 0.8–4.5 mm long, 0.3–0.6 mm wide, clavate, densely papillose above, yellow. PISTILLATE FLOWERS 1 or 2 in each spathe, the spathes 9–14 mm long, 2–4 mm wide; outer tepals 3–4 mm long, 1.6–3 mm wide; inner tepals 4–8.5 mm long, 4–7 mm wide; staminodia clavate, 0.9–2.4 mm long, golden yellow to reddish-orange, densely papillose; hypanthium to 4 cm long, 0.6–0.7 mm wide; ovary at anthesis 2–3 mm long, 1.1–2.2 mm wide, the ovules 6–7, the styles 2.4–3.8 mm long, divided at least 2/3 of their length, white to pale yellow. FRUITS sessile, fusiform, 11.5–14.5 mm long, 4–5.5 mm wide. SEEDS 5.5–7.2 mm long, 1–2 mm wide, the beak 3–3.7 mm long.  $2n = 46$ . [*Anacharis densa* (Planch.) Vict.; *Elodea densa* (Planch.) Casp.].—Still water 1–2 m deep, less common in shallow water and flowing water: Cochise, Maricopa, Pima, Santa Cruz cos.; 350–1,500 m (1,150–5,000 ft.); flowering and fruiting summer to fall; warm-temperate and cool subtropical regions, native to e S. Amer., naturalized worldwide. Commonly used as an aquarium plant.

**ELODEA** Michx.      Waterweed, Ditchmoss

Fresh water perennials, dioecious or rarely monoecious. STEMS usually erect, terete, to 4 m long, usually highly branched near water surface. LEAVES cauline, either prophylls or foliage; prophylls paired, deltate to ovate or narrowly ovate, the apex acute to apiculate,



transparent or pale green; foliage leaves usually paired below, usually in whorls of 3–7 above, ovate to linear or narrowly oblong, spreading or recurved, 1-nerved, the apex obtuse to acute or shortly acuminate, usually bearing more than one minute single celled terminal spine, the base sessile, the margins appearing entire or serrulate to denticulate, with minute single celled teeth. INFLORESCENCES sessile, with a single flower. FLOWERS unisexual, sessile or on long pedicels, (the slender, elongated floral tube or hypanthium pedicel-like) opening above water surface 1 or rarely 2 at a time. STAMINATE FLOWERS sessile to long-pedicellate, remaining attached or becoming free-floating, actinomorphic; outer tepals 3, distinct, green, with lilac to purple stripes or patches of purple, suborbicular to narrowly oblong or narrowly elliptic; inner tepals 3, distinct, very thin and flimsy, deliquescent, whitish-translucent sometimes with a purple vein or tip, rudimentary or usually somewhat longer and distinctly narrower than the outer tepals; stamens usually 9 (or in bisexual flowers usually 3); filaments very short, the inner at least usually united at base forming a column; anther basifixed, oval; pistillodia usually absent, occasionally rudimentary; pollen single or in tetrads. PISTILLATE FLOWERS with outer tepals and inner tepals as in the staminate flowers but usually somewhat smaller; staminodia 3, distinct, filiform, rarely exceeding 2 mm long, greenish white below, lilac above, papillose, usually persisting after the styles have withered; ovary cylindrical 1-locular, with 3–10 ovules, the styles 3. BISEXUAL FLOWERS similar. FRUIT ellipsoidal to ovoid, irregularly dehiscent. SEEDS fusiform, with beak, glabrous to hirsute. [*Anacharis* Rich.].—5 spp., temperate N. Amer. and temperate to subtropical S. Amer. Absent from C. Amer and tropical S. Amer. Widely introduced and naturalized in Eurasia and Australasia. (Greek: *helodes* = marshy, for the habitat). Cook & Urmi-König (1985).

*Elodea canadensis* is unknown from Arizona, but here included in the key because of historic confusion and possible future introduction. In addition, collections labeled as *E. nuttallii* are mis-identified and not included in our flora, the native range of this species lies well outside our borders.

1. Upper leaves usually not imbricate somewhat irregular and spreading, usually linear, parallel-sided, often paired. Staminate flowers with anthers at least in center of flower 4 mm or more long, the pollen released as single grains and pedicels remaining a short time after anthesis. Pistillate flowers with outer tepals rarely more than 2.5 mm long; inner tepals rarely more than 1 mm wide; seeds up to 4 mm long, densely hirsute.....*Elodea bifoliata*
- 1' Upper leaves usually imbricate in regular rows and lying along the stem, often oblong or ovate, rarely paired, usually whorled in threes. Staminate flowers with anthers rarely more than 3 mm long, the pollen usually released in tetrads and pedicels detaching before or during anthesis. Pistillate flowers with outer tepals usually more than 2.5 mm long; inner tepals usually more than 1 mm wide; seeds up to 7.5 mm long, glabrous or rarely sparsely hairy.....  
.....*Elodea canadensis*

***Elodea bifoliata*** H. St. John (two leaved). Two-leaved Waterweed.—LEAVES: prophylls to 2 mm long, to 1 mm wide; foliage leaves often paired, with internodes often longer than the leaves; upper leaves not imbricate, linear to narrowly elliptic or rarely lanceolate, 4.7–25 mm long, 0.8–4.3 mm wide, usually pale green, flat and spreading, the apex acute, the margins mostly straight and parallel. PEDUNCLES to 7 cm long, 0.6 mm wide, usually reaching the water surface, white, flaccid, becoming detached before anthesis. STAMINATE FLOWERS

with outer tepals 2.3–6.1 mm long, 1.2–2.4 mm wide; inner tepals narrowly oblong or oblanceolate 2.7–6.2 mm long, 0.6–1 mm wide; stamens usually 7–9, the inner 3 filaments connate, up to 1.5 mm long; anthers 1.5–4.5 mm long, the pollen in monads. PISTILLATE FLOWERS with outer tepals 1.8–2.7 mm long, 0.8–2.9 mm wide; inner tepals narrowly elliptic or oblanceolate, 2.1–2.8 mm long, 0.6–1 mm wide; staminodia 0.8–1.4 mm long; styles linear, 2.3–3 mm long, bifid for 1/4–2/3 of their length. FRUIT mostly ovate, 6.5–8.0 mm long, 2.3–4.5 mm wide, beak up to 20 mm long. SEEDS narrowly ellipsoidal, 2.8–3.0 mm long, 0.9–1 mm wide, densely covered in white unicellular hairs, 0.5–1 mm long. [*Elodea longivaginata* H. St. John; *E. nevadensis* H. St. John].  $2n = 24$ .—Lakes, ponds and tanks: Apache, Coconino, Greenlee, Navajo, Yavapai cos.; 950–3,050 m (3,200–10,000 ft.); flowering and fruiting summer to fall; higher elevations from Alberta & Saskatchewan s to AZ and NM.

In our area, *Elodea bifoliata* is extremely easy to identify with its hairy seeds. The type of *Elodea bifoliata* is from Lake Mary, Coconino County.

### HYDRILLA Rich.

### Water Serpent

Annuals or perennials of fresh or brackish water, monoecious or rarely dioecious. ROOTS long and simple, adventitious, arising at nodes. STEMS erect, elongate, rhizomatous or stoloniferous, branched or unbranched. LEAVES cauline, sessile, whorled, 3 to 12 per node, linear to lanceolate, rarely widely-ovate or elliptic, 5–20 mm long, 1.2–4 mm wide, with or without reddish brown spots or stripes, the midrib distinct and often bearing unicellular spines on the abaxial surface, the apex acute and terminating with a single spine, the margins usually sparsely serrulate-denticulate, with the teeth usually visible, often spinose. INFLORESCENCES 1-flowered. FLOWERS unisexual, developing within spathes. STAMINATE FLOWERS released underwater as globose buds which open in the air on the surface of the water, the pedicels 0.2–0.5 mm long; outer tepals 3, distinct, imbricate, 1–3 mm long, 1–2 mm wide, whitish-red or brown; inner tepals 3, distinct, linear or spatulate, 1–2 mm long, whitish or reddish; stamens 3, the filaments oblique, 0.25–0.75 mm long, the anthers erect, 4-locular, explosively dehiscent; pistillodes absent. PISTILLATE FLOWERS with a filiform hypanthium, 0.55–10 cm long; outer tepals 3, distinct, oblong-ovate, 1–4 mm long, hyaline, streaked with red or white; inner tepals 3, distinct, 1–3.5 mm long, transparent, occasionally with reddish streaks; staminodes 3, minute or absent, transparent; ovary unilocular, cylindrical, the style 1, the stigmas 3. FRUIT indehiscent, cylindrical, 5–15 mm long, smooth or spiny, the spines lateral, to 3 mm long. SEEDS rarely more than 5, cylindrical, 1.5–2.5 mm long, smooth, glabrous.—A monotypic genus. Cosmopolitan in warmer regions. Cook & Lüönd (1982).

**Hydrilla verticillata** (L. f.) Royal (whorled or verticillate leaves). Water Serpent.—Characteristics of the genus. [*Elodea verticillata* (L. f.) F. Muell.; *Vallisneria verticillata* (L. f.) Roxb.].  $2n = 16, 24, 32$ .—A great number of habitats, but typically in shallow, slow moving water, rarely in swiftly-flowing water or shady areas: Maricopa Co.; 300–350 m (1,000–1,100 ft.); flowering material unknown in AZ. Readily reproduces vegetatively and has become a pest in many areas by restricting water flow in irrigation systems.



**Vallesneria L.**

Wildcelery, Tapegrass, Eelgrass

Perennial herbs of fresh (ours) or salt water, dioecious. ROOTS fibrous. STEMS erect, short, rhizomes and stolons present. LEAVES basal, linear, sessile, strap-shaped, with coloration appearing 3-zoned (a lighter center and darker zones on each end), 3–5-nerved, the apex obtuse to apiculate, the margins entire to finely-toothed. INFLORESCENCES cymose, long-pedunculate. FLOWERS unisexual, developing within spathes, zygomorphic. STAMINATE FLOWERS sessile, released underwater and opening on the surface of the water, the outer tepals 3, the inner tepal 1, minute; stamens 3 (1 staminodia and 2 fertile), the filaments distinct, rarely connate and appearing as one; anthers spheric; pollen in monads. PISTILLATE FLOWERS solitary, pedicellate, floating, the outer tepals 3, the inner tepals 3, minute, transparent; staminodia 3; ovary 1-locular, the styles 1, short or highly reduced, the stigmas 3; ovules numerous. FRUITS cylindrical to ellipsoid, ridged, irregularly dehiscent. SEEDS numerous, ellipsoid, glabrous.  $2n = 20$ .—2 species, 4 varieties, cosmopolitan. (Named for the Italian naturalist, Antonio Vallisneri, 1661–1730). Lowden (1982); Jacobs & Franks (1997); Les et al. (2008).

**Vallisneria americana** Michx. (of America). American wild celery, Tape-grass, Eelgrass.—INFLORESCENCES solitary flowers, racemes or umbellate, the scapes 3–16 cm long, 1.5–5 mm wide. STAMINATE FLOWERS 1–1.4 mm in diam., upright, the stamens with united filaments, with inconspicuous transparent hairs at base. PISTILLATE FLOWERS: outer tepals 3.5–9.5 mm long; staminodia large, conspicuous, the stigmas with reduced styles or adnate to a fused style base, the stigmatic lobes equal.—2 subsp. Amer., e and se Asia, Japan, Oceania and Australia.

Subsp. **americana**.—LEAVES 30–150 cm long, 4–10 mm wide, 3–5-nerved, the margins sub-entire to slightly serrated with minute teeth. STAMINATE FLOWERS with the spathe 1.8–2 cm long; peduncles 3–16 cm long; outer tepals 0.8–1 cm long; filaments partially connate, with a few transparent hairs at base of androecium. PISTILLATE FLOWERS solitary or rarely in a 3–60-flowered umbel to spike-like inflorescence, with regular to irregular flowers; spathe 1.8–2 cm long; peduncles 0.5–2 cm long; outer tepals 4–6 mm long; inner tepals 0.6–0.7 mm long; staminodia 0.4–0.5 mm long, adnate to styles, not to stigmas; style 0.8–1 mm long, the stigma 3–4 mm long. [*Vallisneria asiatica* Miki; *V. neotropicalis* Vict.; *V. spiralis* var. *americana* (Michx.) Torr.].—Still to flowing water, usually up to 1 m or more deep, common in irrigation canals where it hinders water flow: Maricopa, Santa Cruz cos.; 300–1,350 m (1,000–4,400 ft.); fl. unknown in AZ.; throughout N. Amer.; Cuba, Caribbean Mex., Guatemala, Belize and Honduras, to e and se Asia, Oceania and Australia. Cultivated as decorative aquarium plant.

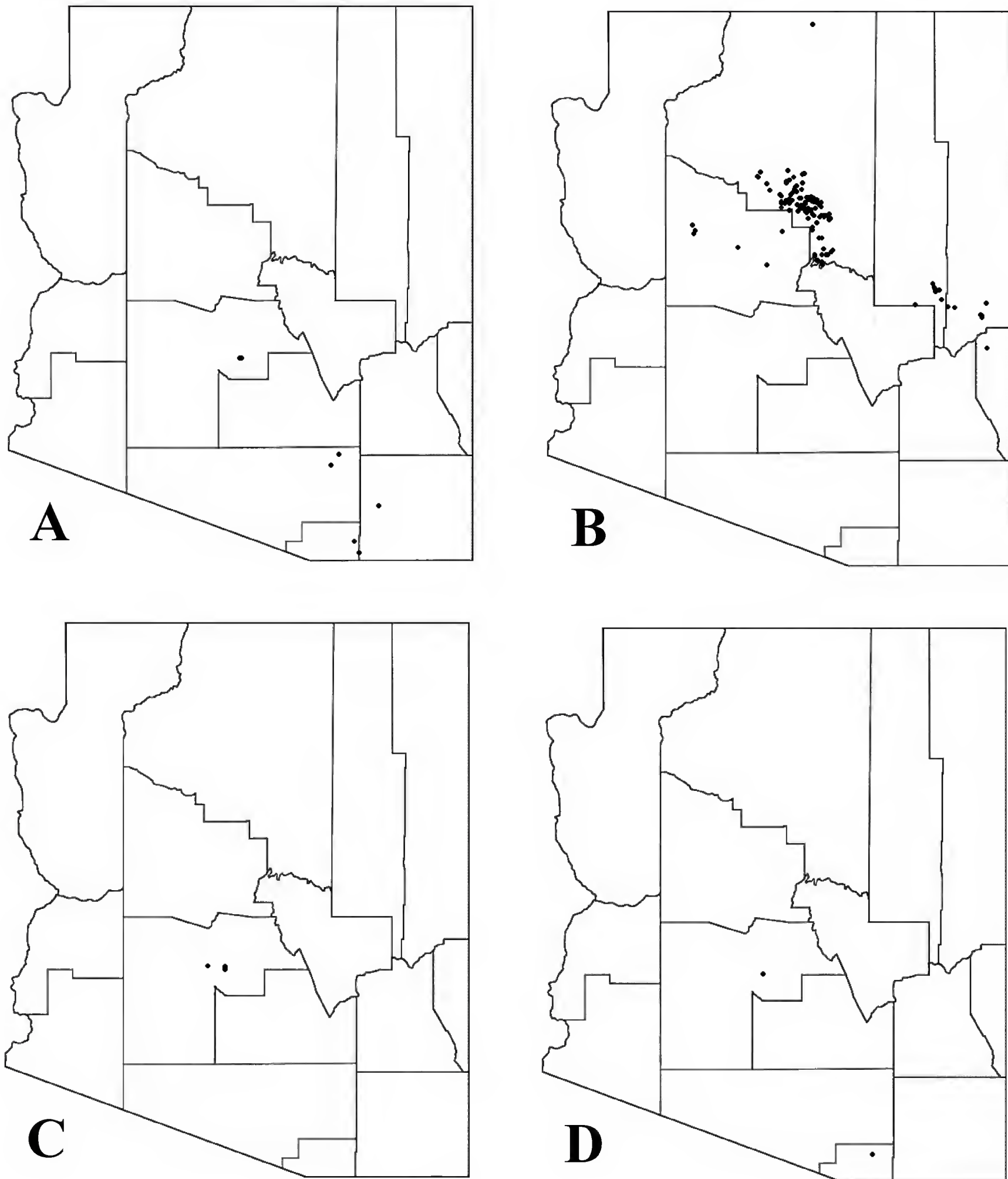
The Arizona collections are from an irrigation canal in Phoenix and Monkey Springs in Santa Cruz County. Flowering collections are unknown in Arizona; however, the species is an aggressive vegetative reproducer.

Les et al. (2008) have been working on *Vallisneria*, resurrecting a few names and describing as many as 6 new species, primary from Australia and Eurasia. However, a comprehensive revision of the entire genus is still needed. Although, it is certain that the material in AZ will remain as *V. americana*, the future subspecies or varietal names may in fact change in time and the above description (based on current understanding of the taxa) may require refining at a later date.

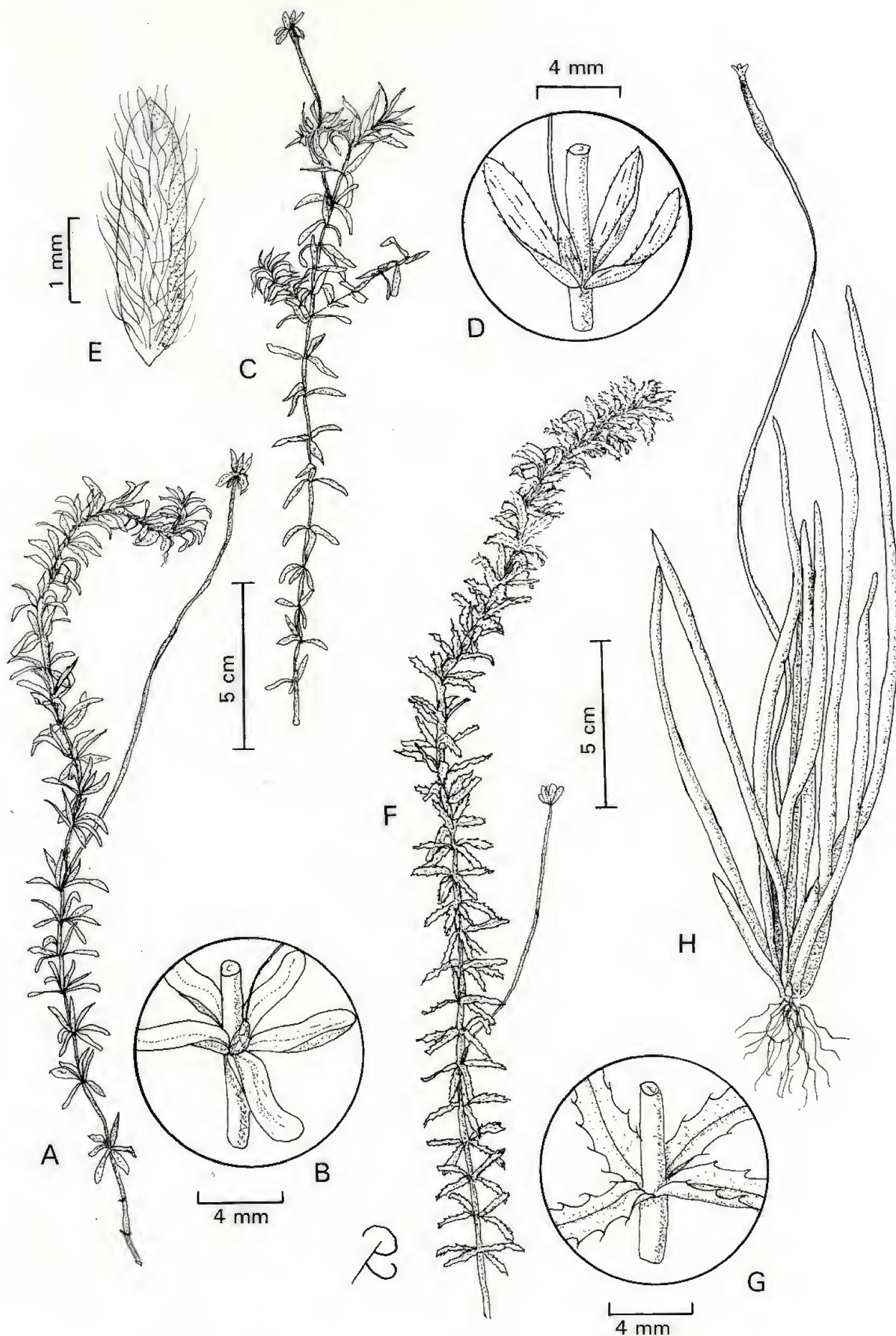


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**Hydrocharitaceae.** Figure 1. Distributions maps. A). *Egeria densa*. B). *Elodea bifoliata*. C). *Hydrilla verticillata*. D). *Vallisneria americana* subsp. *americana*.



**Hydrocharitaceae.** Figure 2. (A–B) *Egeria densa*. A. Habit. B. Detail of stem and leaf whorl arrangement. (C–E) *Elodea bifoliata*. C. Habit. D. Detail of stem and leaf whorl arrangement. E. Seed. (F–G) *Hydrilla verticillata*. F. Habit. G. Detail of stem and leaf whorl arrangement. (H) *Vallesneria americana* subsp. *americana*. H. Habit. [Drawn by Jon Ricketson].



## NAJADACEAE

## WATER-NYMPH FAMILY

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Submerged aquatic annual or rarely perennial herbs, glabrous, monoecious or dioecious. ROOTS fibrous, adventitious at lower nodes. STEMS slender, usually profusely branched distally, the internodes armed with spinulose prickles or unarmed. LEAVES subopposite or appearing verticillate, linear, sessile, 1-veined, the apex acute to acuminate, the margins entire, minutely serrulate; midvein sometimes dorsally armed with spines; sheath deciduous. INFLORESCENCES axillary, solitary, or few flowered cymes, sessile or short-pedunculate, often with an involucrel spathe. STAMINATE INFLORESCENCES: floral bracts absent; peduncles elongating at anthesis. PISTILLATE INFLORESCENCES: floral bracts absent or rarely present, sessile. FLOWERS unisexual. STAMINATE FLOWERS: perianth absent; stamen 1; anther sessile, 1–4-celled, dehiscing irregularly. PISTILLATE FLOWERS: perianth absent; pistil 1, 1-loculed; ovule 1, the placentation basal; styles short, the stigmas 2–4-lobed. FRUITS achene-like, dehiscing by decay, with thin walls, 1-seeded, the seeds fusiform to obovate, often asymmetrical, the testa smooth or with 15 to 60 regular or irregular rows of areolas.—A monogeneric family, ca. 40 spp., nearly worldwide. Haynes (1979, 2000); Lowden (1986).

**Najas** L.      Water-Nymph, Bushy-Pondweed

Characters of the family. – (Greek: *naias* = a water-nymph).

Sterile collections are difficult to determine. However, mature fertile collections are quite easy to separate based on seed architecture.

1. Staminate and pistillate flowers on different plants; leaves and internodes spinulose .....*N. marina*
- 1' Staminate and pistillate flowers on same plants; leaves and internodes without spines.
  2. Testa smooth, but finely reticulate, glossy; seeds obovoid, yellow to brown; anthers 1-celled. ....*N. flexilis*
  - 2' Testa reticulate to pitted, dull; seeds fusiform to ellipsoid, yellowish white to greenish or reddish-brown or with a purple tinge; anthers 1–4-celled.....  
.....*N. guadalupensis*

**Najas flexilis** (Willd.) Rostk. & Schmidt (flexible). Slender Water-Nymph.—Plants monoecious. STEMS flaccid, 2.5–5 cm long, 0.2–0.6 mm wide, unarmed. LEAVES narrowly linear, 0.2–3.6 cm long, 0.2–2.6 mm wide; apex acute to long acuminate, with 1 to 2 minute unicellular terminal teeth; margins serrulate with

35 to 80 minute unicellular teeth per side; midvein unarmed; basal sheath 2–3 mm long, 0.7–1.6 mm wide, the apex rounded, usually with scattered minute unicellular teeth, the margins otherwise entire. INFLORESCENCES with 1 or 2 flowers per leaf axil; involucre beaks 0.7–1.2 mm long, 3-lobed. STAMINATE FLOWERS above the pistillate flowers, 1.1–2.7 mm long; anthers 1.1–2.7 mm long, 1-celled. PISTILLATE FLOWERS below the staminate flowers, 2.5–4.7 mm long; styles 1.5–1.7 mm long; stigmas 3-lobed. SEEDS deep brown to yellow, obovoid, 1.2–3.7 mm long, 0.2–1.2 mm wide; testa glossy, smooth but finely reticulate, the areolas regularly arranged in ca. 50 longitudinal rows.  $2n = 12, 24$ . [*Caulinia flexilis* Willd.].—Ponds: Yavapai Co.; ca. 1100 m (3600 ft.); flowers and fruits summer-fall; N. Amer., Eurasia.

Both *Najas flexilis* and *N. guadalupensis* subsp. *guadalupensis* have been collected in the Page Springs Fish Hatchery at Cornville in Yavapai County.

**Najas guadalupensis** (Spreng.) Mangus (from Guadalupe). Common Water-Nymph.—Plants monoecious. STEMS flaccid, 11–90 cm long, 0.1–2 mm wide, unarmed. LEAVES narrowly linear, 0.3–3.3 cm long, 0.2–2.1 mm wide; apex obtuse to acute, with 1 to 3 minute unicellular terminal teeth; margins serrulate with 18 to 100 minute unicellular teeth per side; midvein unarmed; basal sheath 3–5 mm long, 1–3.4 mm wide, the apex rounded to truncate, the margins usually with a few teeth, sometimes entire. INFLORESCENCES with 1 to 3 flowers per leaf axil; involucre beaks 0.2–1.3 mm long, 4-lobed. STAMINATE FLOWERS above the pistillate flowers, 1.5–3 mm long; anthers 1–1.7 mm long, 1- to 4-celled. PISTILLATE FLOWERS below the staminate flowers, 1.5–4 mm long; styles 0.3–1.5 mm long; stigmas 4-lobed. SEEDS whitish yellow with purple tinge, fusiform to ellipsoid, 1.2–3.8 mm long, 0.4–0.8 mm wide; testa dull, reticulate to pitted, the areolas regularly arranged in 20 to 60 longitudinal rows.  $2n = 12, 36, 42, 48, 54, 60$ . [*Caulinia guadalupensis* Spreng.].—4 subspp. New World.

Subsp. **guadalupensis**.—STEMS 11–75 cm long, 0.1–0.8 mm wide. LEAVES 0.3–2.8 mm long, 0.2–1.8 mm wide; apex acute to mucronate; margins with 50 to 100 minute unicellular teeth per side that are invisible to unaided eye. STAMINATE FLOWERS 1.5–2.4 mm long; anthers 4-celled. PISTILLATE FLOWERS 1.5–2 mm long. SEEDS 1.2–2.5 mm long, 0.4–0.6 mm wide, the areolas in 20 longitudinal rows.  $2n = 24$ .—Lakes and tanks: Coconino, Maricopa, Pima, Pinal, Santa Cruz and Yavapai cos.; 1100–1500 m (3600–5000 ft.); flowers and fruits summer-fall; throughout New World.

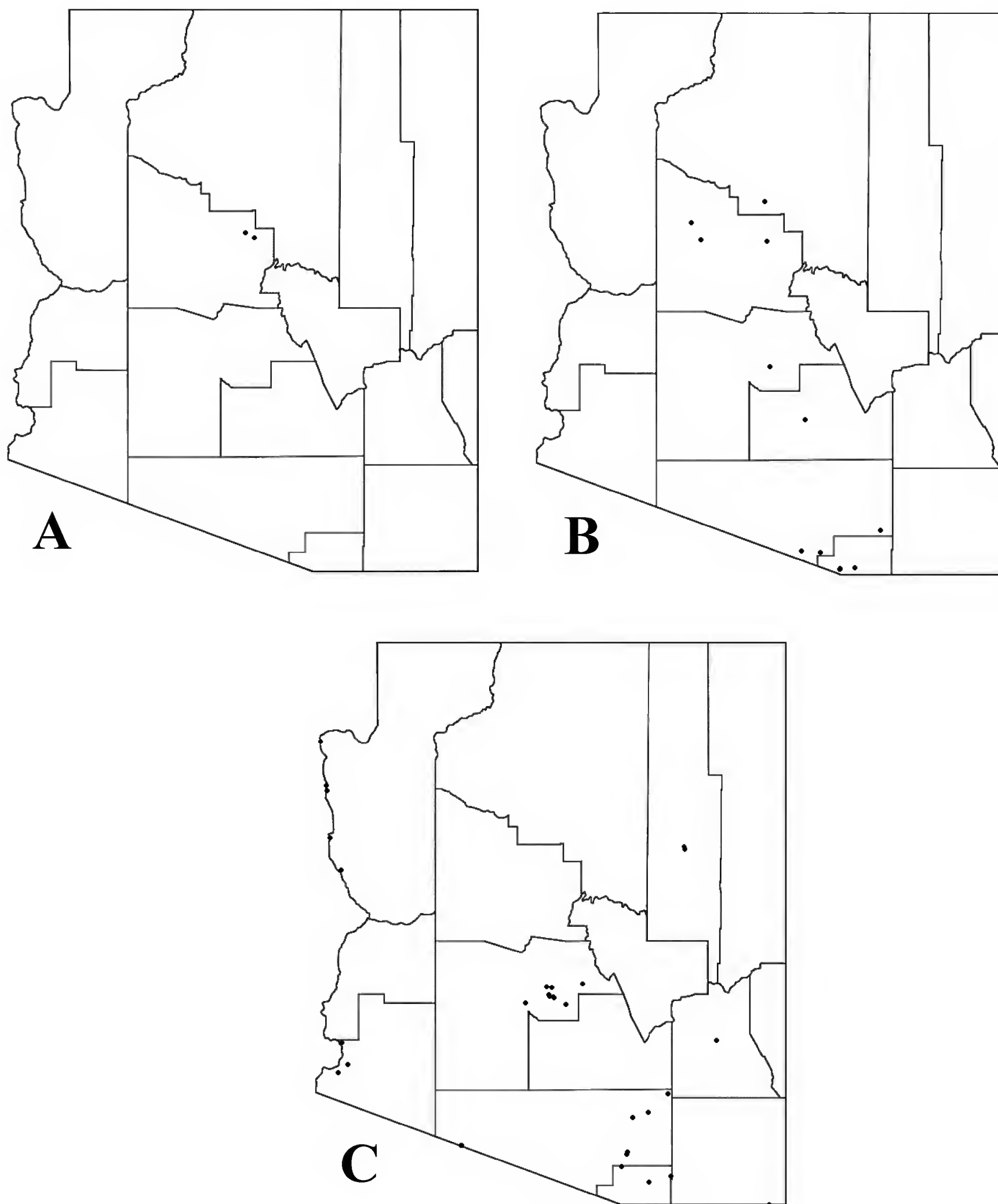
**Najas marina** L. (of the sea). Holly-Leaved Water-Nymph.—Plants dioecious. STEMS stout, 6–45 cm long, 0.4–5 mm wide, usually armed with spinulose prickles. LEAVES narrowly linear, 0.5–3.9 cm long, 0.4–4.5 mm wide; apex acute, with a terminal spinulose prickles; margins coarsely serrate with 8 to 13 stiff multicellular teeth tapering to a sharp spiny point; midvein armed abaxially with spinulose prickles; basal sheath 5–6 mm long, 2–4.4 mm wide, the apex acute to rounded, the margins entire or with a few teeth. INFLORESCENCES with 1 flower per leaf axil; involucre beaks 0.3–0.7 mm long, 2-lobed. STAMINATE FLOWERS scattered throughout, 1.7–3 mm long; anthers 1.7–3 mm long, 4-celled. PISTILLATE FLOWERS scattered throughout, 2.5–5.7 mm long; styles 1.2–1.7 mm long; stigmas 3-lobed. SEEDS

reddish-brown, ovoid, 2.2–4.5 mm long, 1.2–2.2 mm wide; testa dull, pitted, the areoles irregularly arranged, not in distinct rows.  $2n = 12$ . [*N. gracilis* Morong].—Lakes, ponds, springs, ditches, streams and rivers; Cochise, Graham, Maricopa, Mohave, Navajo, Pima, Santa Cruz and Yuma cos.; 300–1550 m (1000–5000 ft.); flowers and fruits summer-fall; throughout New World and Eurasia.

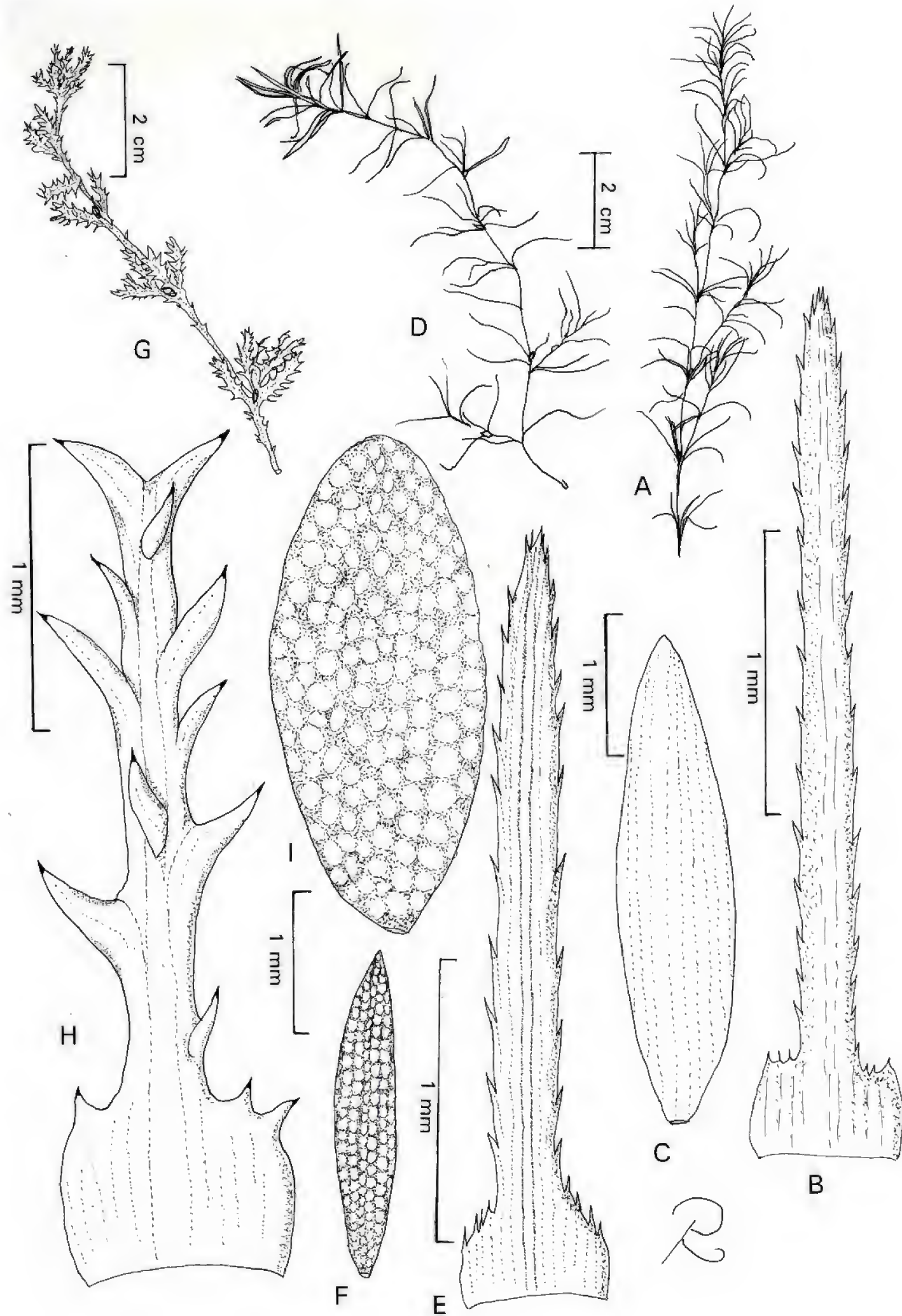
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**Najadaceae.** Figure 1. Distribution maps. A) *Najas flexilis*. B) *Najas guadalupensis* subsp. *guadalupensis*. C) *Najas marina*.



**Najadaceae.** Figure 2. *Najas*. (A–C) *N. flexilis*. A) Flowering branch. B) Leaf. C) Seed. (D–F) *N. guadalupensis* subsp. *guadalupensis*. D) Flowering branch. E) Leaf. F) Seed. (G–I) *N. marina*. G) Flowering branch. H) Leaf. I) Seed. [Drawn by Jon Ricketson].



## RESEDACEAE MIGNONETTE FAMILY

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Annual, biennial, or perennial herbs or shrubs. STEMS erect or ascending. LEAVES simple, alternate or fasciculate, entire to deeply lobed; stipules gland-like. INFLORESCENCES terminal racemes or spikes. FLOWERS perfect, bracteate, irregular and asymmetric; sepals 2 to 8, persistent or deciduous, distinct or basally connate; petals 0-8, small, distinct or connate; stamens 3-many, the filaments distinct to connate; pistils 2-8, basally connate, each with a beak-like stigma; ovary superior, unilocular; ovules 1-many per locule. FRUITS capsules. SEEDS few to many, reniform.—6 genera, 70 spp., chiefly Medit.

### **Oligomeris** Camb.      Whitepuff

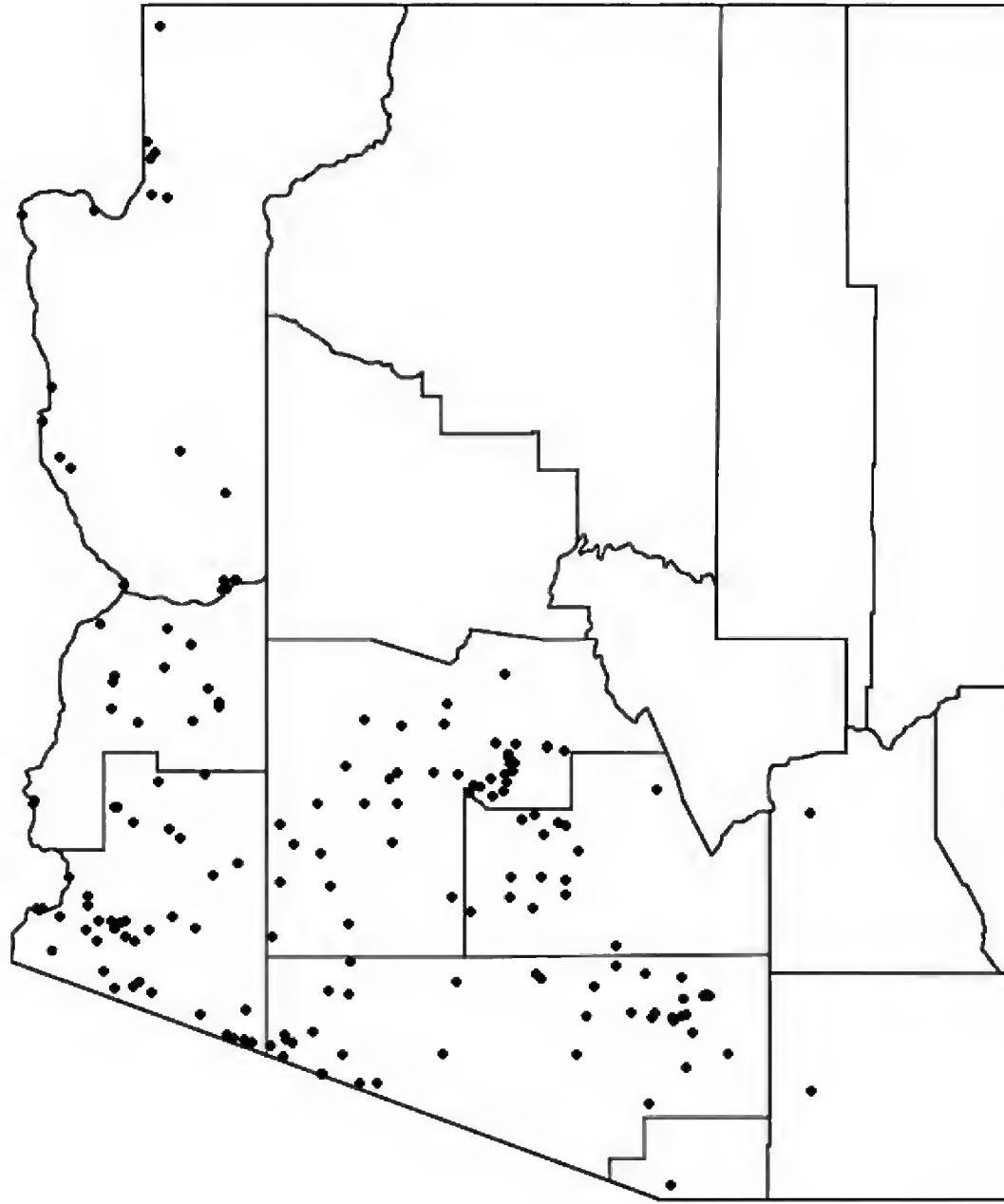
Annual or perennial herbs. LEAVES alternate, sometimes appearing fasciculate; blades entire, or sometimes toothed near the base. INFLORESCENCES spikes. FLOWERS: sepals 2–6, persistent, distinct, white-margined; petals 2–3, distinct to basally connate, entire to shallowly lobed; stamens 3-10; filaments persistent, distinct or basally connate; ovaries 4(–5)-carpellate. FRUITS erect, subglobose to obovoid, opening with an apical pore, the walls membranous. SEEDS smooth, shiny.—3 spp.; sw N. Am., n Mex., sw & c Asia, Afr. (Greek: few parts).

***Oligomeris linifolia*** (Vahl) Macbr. (flax-leaved). Flaxleaf whitepuff.—Annual herbs, glabrous, somewhat succulent or fleshy. ROOTS taprooted. STEMS erect, to 45 cm, branching from base. LEAVES sessile, linear to narrowly oblanceolate, 8–50 mm long, 0.5–2 mm wide. INFLORESCENCES 4–16 cm long; bracts persistent, 1–1.5 mm long, triangular or subulate. FLOWERS sessile, to 2 mm long; sepals 4, ovate-lanceolate to deltate; petals 2, white, ovate, distinct or sometimes basally connate; stamens 3, the filaments to 1 mm long. FRUITS subglobose, with 4 teeth at apex. SEEDS black or brown, shiny, ca. 25–30 per fruit, 0.5–0.7 mm long.  $2n = 30$ . [*Reseda linifolia* Vahl].—Salt and clay flats, boulders and gravel bars in arroyos and along rocky slopes, roadsides: Cochise, Graham, La Paz, Maricopa, Mohave, Pima, Pinal, Santa Cruz, Yuma cos.; below 1200 m (3600 ft); Feb–Aug; CA, NM, NV, TX; Mex.; sw & c Asia, n Afr.

Recent molecular work suggests the species is native to North America, despite a substantial disjunction from other populations in Africa and Asia (Martin-Bravo et al. 2009).

**LITERATURE CITED**

MARTIN-BRAVO, S., R. VARGAS, M. LUCEÑO. 2009. Is *Oligomeris* (Resedaceae) indigenous to North America? Molecular evidence for a natural colonization from the Old World. *American Journal of Botany* 96(2): 507-518.



**Resedaceae.** Figure 1. Distribution of *Oligomeris linifolia*.



**Resedaceae.** Figure 2. *Oligomeris linifolia*. A. Scan of whole plant (*Landrum 10903*, ASU). B. Close up of spikes with flowers at apex and fruits below (*Landrum 12020*, ASU).



## RUPPIACEAE

## DUTCHGRASS FAMILY

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Submerged aquatic herbs, annual or rarely perennial. STEMS erect in water column, filiform, simple, or branched. LEAVES alternate to subopposite, linear-filiform, delicate, sessile, with a non-persistent stipular sheath. INFLORESCENCES terminal spikes, at first enclosed in a spathe, pedunculate, the peduncles elongating after fertilization to the water surface, often spiraling; bracts absent. FLOWERS bisexual; perianth absent; stamens 2, the filaments short, broad, the anthers extrorse, 2-celled, dehiscing longitudinally; pistils 4 to 16, sessile at anthesis; ovary with a single parietal ovule. FRUITS small, drupaceous, indehiscent, on a long slender stipe that continues to elongate and spiral as the fruit matures; seed 1.—A monogeneric family, ca. 10 spp., worldwide. Haynes (2000).

### **Ruppia** L.     Ditchgrass

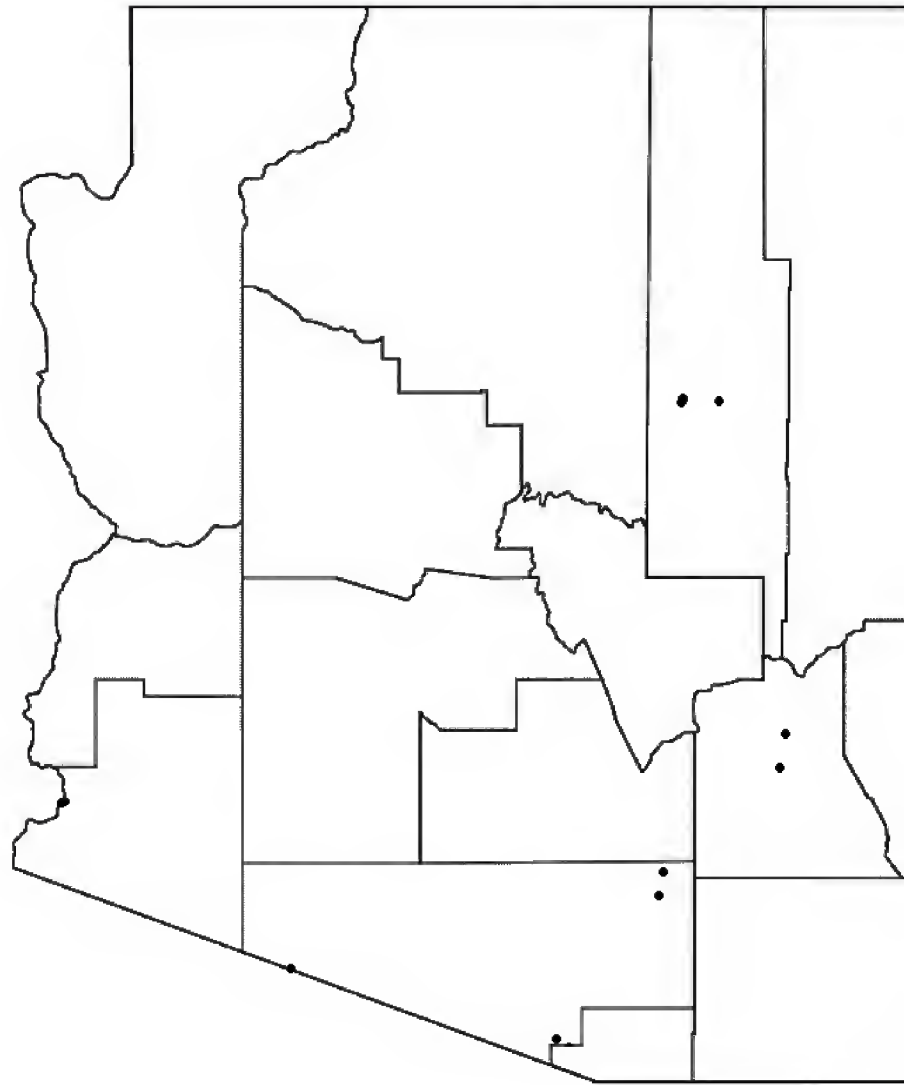
Characters of the family.—(named in honor of Heinrich Bernhard Ruppius, 1689–1719, a German Botanist and the author of the *Flora Jenensis*).

**Ruppia cirrhosa** (Petagna) Grande (tendrilled). Spiral Ditchgrass. —Submerged annuals. STEMS to 55 cm long, 0.1–0.3 mm wide, greenish to brownish. LEAVES 3.2–45 cm long, 0.2–0.5 mm wide, apically acute, the margins entire at the base, minutely serrulate near the apex, 1-nerved. INFLORESCENCES fewer than 20-flowered; peduncles with 5 to 30 coils, 3–30 cm long, 0.05 cm wide. FLOWERS with stamens early deciduous; pistils 4 to 6. FRUITS 1.5–2 mm long, 1.1–1.5 mm wide; gynophore 2–3.5 cm long; beak lateral, erect, 0.5–1 mm long.  $2n = 40$  [from Eur. material]. [*Buccaferrea cirrhosa* Petagna].—Lakes and ponds: Graham, Navajo, Pima, Yuma cos.; 50–450 m (160–1500 ft.); flowering and fruiting summer-fall, overwintering in some warm locations); throughout N. Amer. and Eur.

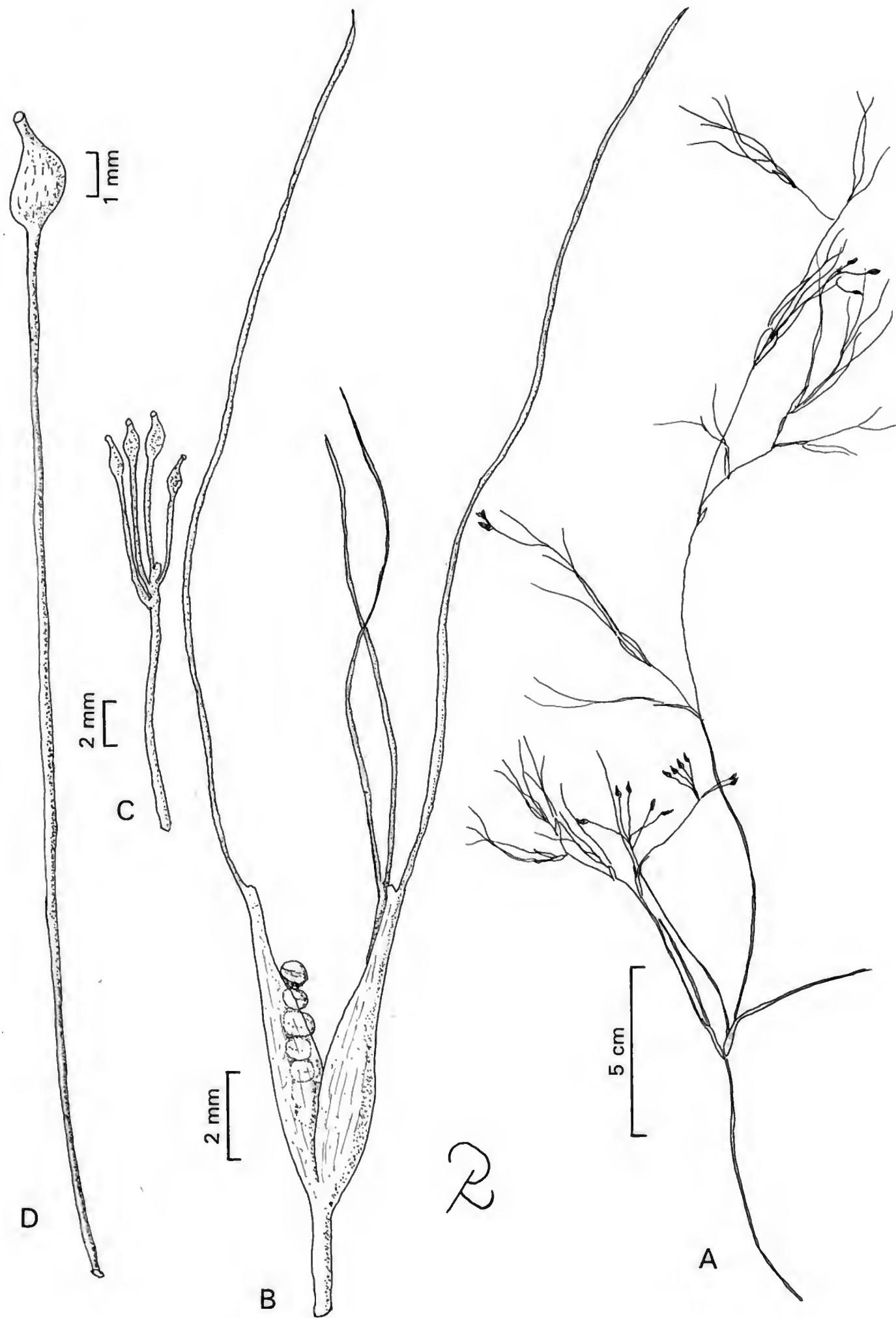
Until recently, in AZ, this entity has been called *Ruppia maritima* L., a primarily coastal species with shorter peduncles in fruit and with fewer coils. However, our material is better referred to *R. cirrhosa*, the more commonly known European species.

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HAYNES, R. R. 2000. Ruppiaceae. Pp. 76–77. In: Flora of North America Editorial Committee (eds.). *Flora of North America north of Mexico*. Vol. 22. New York: Oxford University Press.



**Ruppiaceae.** Figure 1. Distribution of *Ruppia cirrhosa*.



**Ruppiaceae.** Figure 2. *Ruppia cirrhosa*. A) Habit. B) Flowering branch (incl. a spicate inflorescence partially enclosed in a spathe and emerging new leaves). C) Cluster of single-carpel fruits from one flower. D). Single stalked fruit of one carpel. [Drawn by Jon Ricketson].



## SCROPHULARIACEAE

## FIGWORT FAMILY

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Herbs or shrubs. LEAVES simple, alternate or opposite, with or without glands; stipules absent. INFLORESCENCE racemose or cymose or flowers solitary and axillary. FLOWERS perfect, actinomorphic to zygomorphic, ebracteate, hypogynous; sepals 5, united, the lobes equal or unequal and shorter than the tube; petals 5, united, the corolla regular to 2-lipped, the upper lip 2-lobed, external in bud, the lower lip three-lobed; stamens 2–5, all with two well-developed anther sacs, or with staminodes sometimes present, the thecae confluent at the apex; carpels 2, fused, superior; locules 2; placentation axile; style solitary and terminal; stigmas 2-lobed, the lobes distinct or united. FRUIT a 2-valved, septicidal capsule, berry or drupe.—ca. 60 genera, ca. 1800 spp., worldwide.

Many of the 300+ genera in the Scrophulariaceae s.l. are now placed in other families because recent studies show that the family is not monophyletic (APG IV 2016). The families are difficult to separate morphologically and many authors have yet to embrace the taxonomic changes. We use the more narrowly circumscribed family here to be consistent with the treatment in preparation for Flora of North America.

1. Shrubs; inflorescence a compact cyme ..... *Buddleja*
- 1' Herbs; inflorescence a spike, raceme, panicle, or solitary flower.
  2. Plants aquatic or semi-aquatic, acaulescent; flowers solitary in leaf axils ..... *Limosella*
  - 2' Plants terrestrial, caulescent erect; flowers in panicles or racemes.
    3. Leaves alternate; inflorescence a spike or raceme; flowers generally yellow ..... *Verbascum*
    - 3' Leaves opposite; inflorescence a panicle; flowers bi-colored, generally red to purple and green ..... *Scrophularia*

### **Buddleja** L. Butterfly Bush

A genus previously treated as in a separate family. See E. M. Norman (1992; [http://www.canotia.org/vpa\\_volumes/VPA\\_JANAS\\_1992\\_Vol26\\_1\\_Norman\\_Buddlejaaceae.pdf](http://www.canotia.org/vpa_volumes/VPA_JANAS_1992_Vol26_1_Norman_Buddlejaaceae.pdf)).

### **Limosella** L. Mudwort

Rich Crawford

Aquatic to semi-aquatic annual or perennial herbs. STEMS very short, occasionally forming stolons. LEAVES few to many, basal and forming clusters at the

nodes of stolons, petiolate with a hyaline margin at the base; blades linear to spatulate, entire, glabrous, or with sparse minute glandular hairs. FLOWERS small, solitary, pedunculate in leaf axils; calyx campanulate, regular, 5-lobed; corolla actinomorphic or zygomorphic, white to pale pink, glabrous or pubescent on the inner surface, the lobes acute or rounded; stamens 4, +/- equal; style straight or reflexed, persistent or deciduous, the stigma capitate. CAPSULES ovoid; seeds brown, oblong, reticulated with longitudinal grooves. 15 species worldwide.

1. Corolla lobes blunt, style 0.6–1.1 mm long; seeds dark brown.....*L. acaulis*
- 1' Corolla lobes acute, style 0.1–0.6 mm long; seeds light brown.
  2. Inner corolla densely pubescent, plants of Cochise county ..... *L. pubiflora*
  - 2' Inner corolla glabrous, plants mostly distributed N of the Mogollon rim .....  
..... *L. aquatica*

***Limosella acaulis*** Sessé & Moc. (stemless). Owyhee Mudwort.—STEMS none or forming stolons 0–2 cm long. LEAVES linear to linear spatulate, 1–4 cm long; blade 0.25–1.5 mm wide. FLOWERS with peduncle 1.5–8(–12) mm long; calyx 1.5–2.5 mm long; corolla actinomorphic, 1.5–3 mm long, glabrous inside, the limb 0.5–1 mm long; style 0.6–1.1 mm long, persistent. CAPSULES 2–3 mm long; seeds dark brown.—Semi-aquatic habitats near lakes, ponds, and cattle tanks. Apache, Coconino, and Santa Cruz cos., 1920–2606 m (6300–8550 ft), Jun–Oct. AZ, CA, ID, NM, NV, OR.

***Limosella aquatica*** L. (referring to aquatic habit). Water Mudwort.—STEMS none or forming stolons 0–4 cm long. LEAVES linear to ovoid spatulate, 1–8(–20) cm long; blade 0.25–8 mm wide. FLOWERS with peduncle 1.6–10(–25) mm long; calyx 2–3 mm long; corolla actinomorphic or zygomorphic, 2–3 mm long, glabrous inside, the limb 0.5–1 mm long; style 0.1–0.7 mm long, deciduous. CAPSULES 2.5–3 mm long; seeds light brown.—Semi-aquatic and aquatic habitats in and near lakes, ponds, and cattle tanks. Apache, Coconino, and Graham cos., 2060–2925 m (6760–9600 ft), May–Oct. w U.S., circumboreal in the n Hemisphere.

***Limosella pubiflora*** Pennell (pubescent petals). Chiricahua Mudwort.—STEMS none or forming stolons 0–4 cm long. LEAVES linear to ovoid spatulate, 1–8 cm long; blade 0.25–5 mm wide. FLOWERS with peduncle 4–13 mm long; calyx 2–3 mm long; corolla weakly zygomorphic, 2–3 mm long, densely pubescent inside, the limb 0.5–1 mm long; style 0.4–0.6 mm long, deciduous. CAPSULES 2.5–3 mm long; seeds light brown.—In fine silt and mud along small drainages in the Chiricahua Mts., Cochise Co., 1525–1800 m (5000–6000 ft), Feb–May. AZ, NM.

*Limosella pubiflora* is very similar to *L. aquatica* and may be a regional variant.

**Scrophularia** L. Figwort

Rich Crawford

Perennial herbs. LEAVES cauline, opposite to decussate, petiolate, lanceolate to ovate, cordate to cuneate; apex acute; margins coarsely and irregularly dentate to finely serrate. INFLORESCENCE paniculate. FLOWERS perfect; pedicels fine or thickened, flexuous to rigid, pendulous to erect; calyx nearly regular, of 5 subequal lobes, the lobes blunt to acute, the margins usually scarious rarely herbaceous; corolla irregular, throat slightly constricted, the upper lip 2-lobed, red, exceeding lower 3 lobes, the lower 3 lobes bicolored, usually red, white and sometimes green; anther-bearing stamens 4, included or exserted; staminode 1, club-shaped or two-lobed; stigma club-shaped, often becoming reflexed after pollination. CAPSULES ovoid; seeds brown, ovoid, ridged. 150–200 species: N. Amer., temperate Asia, Medit. (Latin: associated with the disease scrofula)

1. Corolla 5–8 mm long; pedicels flexuous; plants widespread in AZ ..... *S. parviflora*  
 1' Corolla 8–10 mm long; pedicels thickened and straight; plants from ne AZ .....  
 ..... *S. lanceolata*

***Scrophularia lanceolata*** Pursh (for leaf shape). Lanceleaf Figwort.—STEMS erect. LEAVES 4–8.5 cm long, 3.5–5 cm wide, cuneate at the base; margins coarsely irregularly dentate. INFLORESCENCE of sub-opposite, paniculate clusters usually 2 per node diverging at 45° angles. FLOWER pedicels thickened, spreading to erect; calyx 2–3 mm long; corolla 8–9 mm long; staminode lobed. CAPSULES 6–7 mm long.—Moist shady places, Apache Co.; Jul–Sep. Widespread in N Amer. except in the se U.S.

This species is known from one collection (D. Roth 156, NAVA) along Teec Nos Pos Creek in the Carrizo Mts.

***Scrophularia parviflora*** Woot. & Standl. (small-flowered). Pineland Figwort.—STEMS erect becoming decumbent with age. LEAVES 4–15 cm long, 1.5–6.5 cm wide, cordate to cuneate at the base; margins coarsely and irregularly dentate to finely serrate. INFLORESCENCE of loose terminal panicles. FLOWER pedicels fine, flexuous, pendant to erect; calyx 2–3 mm long; corolla 5–8 mm long; staminode narrow, club shaped. CAPSULES ovoid, 5–6 mm long.—Moist shady places, common along riparian corridors above 5000 ft: Cochise, Coconino, Gila, Graham, Greenlee, Mojave, Pima, Pinal, Santa Cruz and Yavapai cos., 950–2750 m (3100–9100 ft); Apr–Oct. AZ and sw NM.

*Scrophularia californica* was mistakenly included in the Arizona flora (Kearney & Peebles) but we do not believe that it grows in AZ. It is restricted to coastal ranges and moist canyons of interior mountain ranges in CA and OR. It has larger flowers (7–12 mm long) than *S. parviflora* (5–8 mm long).



**Verbascum** L. Mullein

Katherine Noonan

Biennial herbs, glabrous or sparsely glandular, to densely wooly. STEMS erect, round in cross section. LEAVES simple, alternate, sessile, lanceolate to obovate, clasping or decurrent, rounded, cuneate, entire or toothed, green, glabrous, glandular, to densely wooly, the basal leaves in a rosette, the cauline leaves decreasing in size along the stem. FLOWERS in terminal racemes, pedicellate or subpedicellate; calyx regular, green, glandular-pubescent, 5-lobed, the lobes lanceolate; corolla slightly irregular, rotate, yellow, rarely white, 5-lobed, the upper 2 lobes shorter than lower 3; anther-bearing stamens 5, exserted, the filaments usually villous, or the lower 2 glabrous to sparsely villous, the anthers one-celled; style exserted, the stigmas fused, spherical. CAPSULES ovoid to spherical, glandular to puberulent; seeds oblong, with longitudinal ribs.—Ca. 360 species; Eurasia, 18 species naturalized throughout North America. (Latin for bearded).

1. Leaves entire, wooly; flowers crowded; filaments of stamens glabrous or sparsely villous, yellow..... *V. thapsus*
- 1' Leaves crenate or dentate, glabrous to sparsely pubescent; flowers diffuse; filaments of stamens densely villous, purple.
2. Stems glabrous or nearly so; hairs glandular when present, not forked; pedicels 6–17 mm long, longer than calyx ..... *V. blattaria*
- 2' Stems pubescent, hairs not glandular, forked; pedicels 2–5 mm long, shorter than calyx ..... *V. virgatum*

***Verbascum blattaria*** L. (for control of cockroaches?). Moth Mullein.—STEMS erect, 40–100(–120) cm tall, glabrous below, minutely glandular-puberulent above. LEAVES glabrous; basal leaves oblanceolate to obovate, 4–18 cm long, 1–6 cm wide, the apex acute to rounded, the margins crenate to dentate; cauline leaves oblanceolate to lanceolate, becoming reduced above. FLOWERS pedicellate, the pedicels 6–17 mm; calyx glabrous, 4–8 mm long; corolla 20–30 mm in diameter, yellow or rarely white; filaments 3–5 mm long, purple and white, villous; style 6–9 mm long. CAPSULES subspherical, widest at the base, 7–9 mm long, 6–8 mm wide, glandular-puberulent.—Moderately moist areas, often in drainages or adjacent to farmland or riparian areas: Cochise, Coconino, Yavapai cos., 1020–2165 m (3350–7000 ft); Jun–Oct. In all 50 states, excluding AK, WY, and MN; naturalized from Eurasia, now cosmopolitan.

While not as popular in folk medicine as *Verbascum thapsus*, *V. blattaria* has been shown to exhibit antibacterial properties, and is said to be an effective insecticide (Meurer-Grimes et al. 1996). In Dr. Beal's seed viability experiment, *V. blattaria* seeds germinated after 120 years of dormancy—one of the longest dormancies on record (Telewski and Zeevaart 2002).

*Verbascum thapsus* L. (From the island of Thapsos). Common mullein.—STEMS erect, 30–200 cm tall, wooly. LEAVES densely white wooly; basal leaves oblanceolate, 8–50 cm long, 2.5–14 cm wide, the apex acute to rounded, the margins entire; cauline leaves oblanceolate to elliptic, reduced above. FLOWERS sessile to subsessile; pedicels less than 2 mm long; calyx densely wooly, 8–12 mm long; corolla 15–30 mm in diameter, yellow or rarely white; filaments 3–8 mm long, the upper 3 villous, the lower 2 glabrous to sparsely villous; style 4–7 mm long. CAPSULES egg shaped, 8–11 mm long, 6–9 mm wide, densely tomentose.—Roadsides, waste places, open meadows, rocky hillsides, burned and disturbed places: Apache, Cochise, Coconino, Gila, Graham, Greenlee, Maricopa, Mohave, Navajo, Pima, Pina, Yavapai cos., 355–2,895 m (1165–9500 ft); May–Oct. In all 50 states; naturalized from Eurasia, now cosmopolitan.

*Verbascum thapsus* is listed as a noxious weed in Colorado and Hawaii. This species was intentionally brought to North America by early European settlers, possibly because of its reported medicinal properties. Riaza et al. (2013) review the chemistry and medicinal uses of this species.

In North America, *Verbascum thapsus* displays a wide variety of morphological and life history traits. While usually a monocarpic biennial, populations in the s United States act as annuals, and plants in n latitudes prolong life and delay reproduction until the third year (Reinartz 1984). Morphologically, *V. thapsus* usually produces a single inflorescence stalk, but can sometimes have several lateral branches. These branches develop after the main stem has flowered, and are thought to be a result of infestation by a weevil, *Gymnaetron tetrum* (Naber and Aarseen 1998). The weevil oviposits in the fruit, destroying at least half of the seeds, usually in the early part of the flowering season (Naber and Aarseen 1998). *Verbascum thapsus* individuals in nutrient-rich areas sometimes produce lateral branches, and thus have a greater chance at reproductive success (Naber and Aarssen 1998).

Some *Verbascum thapsus* plants exhibit a rare mutation of the stem tip, called fasciation. The apex of the stem becomes widened, twisted, and markedly large. Fasciation occurs in over 100 plant families, and is perhaps most famous in the crested Saguaro (Ansari and Daehler, 2011). Fasciation can be caused by simple Mendelian inheritance, by a bacterial pathogen, *Rhodococcus fascians*, or by environmental factors, such as overcrowding of roots (Ansari and Daehler 2011). Ansari and Daehler (2011) believe fasciation in *V. thapsus* is most likely due to a combination of environmental conditions and genetics, though the study was unable to investigate which conditions and genes are responsible.

*Verbascum virgatum* Stokes (twiggy). Wand mullein.—STEMS erect, 60–120 cm tall, pubescent. LEAVES puberulent, with forked hairs; basal leaves oblanceolate to obovate, 8–20 cm long, 1.4–4 cm wide, the apex acute to rounded, the margins crenulate to dentate; cauline leaves lanceolate, becoming reduced above. FLOWERS pedicellate, the pedicels 2–5 mm long; calyx stipitate-glandular, 4–7 mm long; corolla 22–30 mm in diameter, yellow; filaments (3–)5–10 mm long, purple and white, villous; style 6–9 mm long. CAPSULES subspherical to spherical, 5–9 mm long, 6–8 mm wide, glandular-puberulent.—Moderately moist roadsides and waste places:



Apache, Cochise, Coconino, Graham, Maricopa, Santa Cruz, Yavapai cos., 610–2100 m (2000–6900 ft), May–Oct; naturalized from Eurasia.

This taxon is far less invasive than *Verbascum thapsus* and *V. blattaria*. It is often confused with *V. blattaria*, but can be distinguished based on a pedicel length of 2–5 mm (vs. 6–17 mm in *V. blattaria*).

#### ACKNOWLEDGMENTS

We would like to thank Patrick Alexander, Steve Buckley, and Glen Clifton for valuable information regarding *Limosella*. Tracy Tohanne provided to the illustrations. Max Licher and Steve Buckley provided field photos. We thank the staff of ARIZ, ASC, ASU, and DES for their assistance with loans.

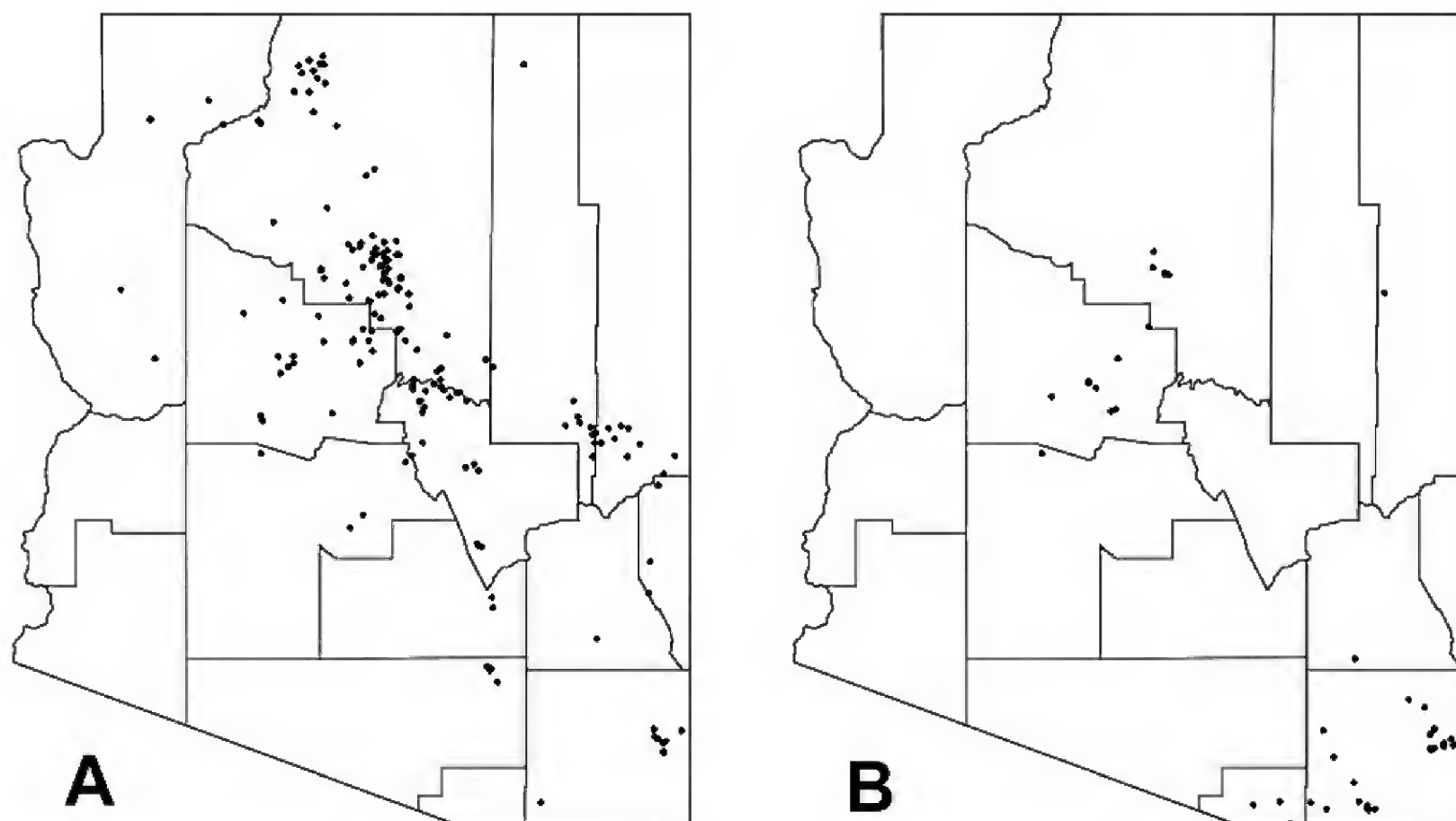
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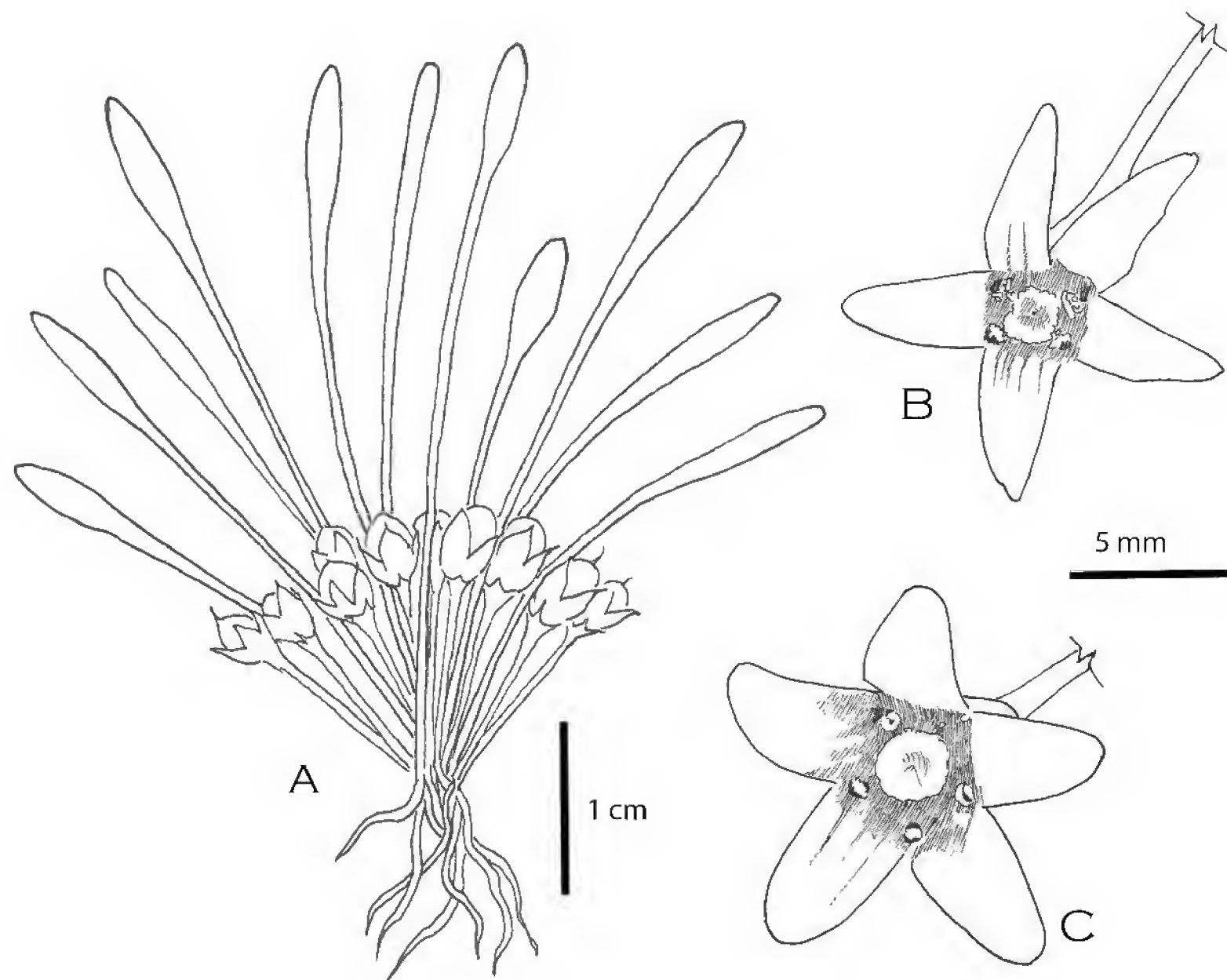




**Scrophulariaceae.** Figure 1. Distribution of: (A) *Limosella acaulis*; (B) *L. aquatic* (circles) and *L. pubiflora* (square in se corner of AZ); (C) *Scrophularia lanceolata* (square in ne corner of AZ) and *S. parviflora* (circles); (D) *Verbascum blattaria*.

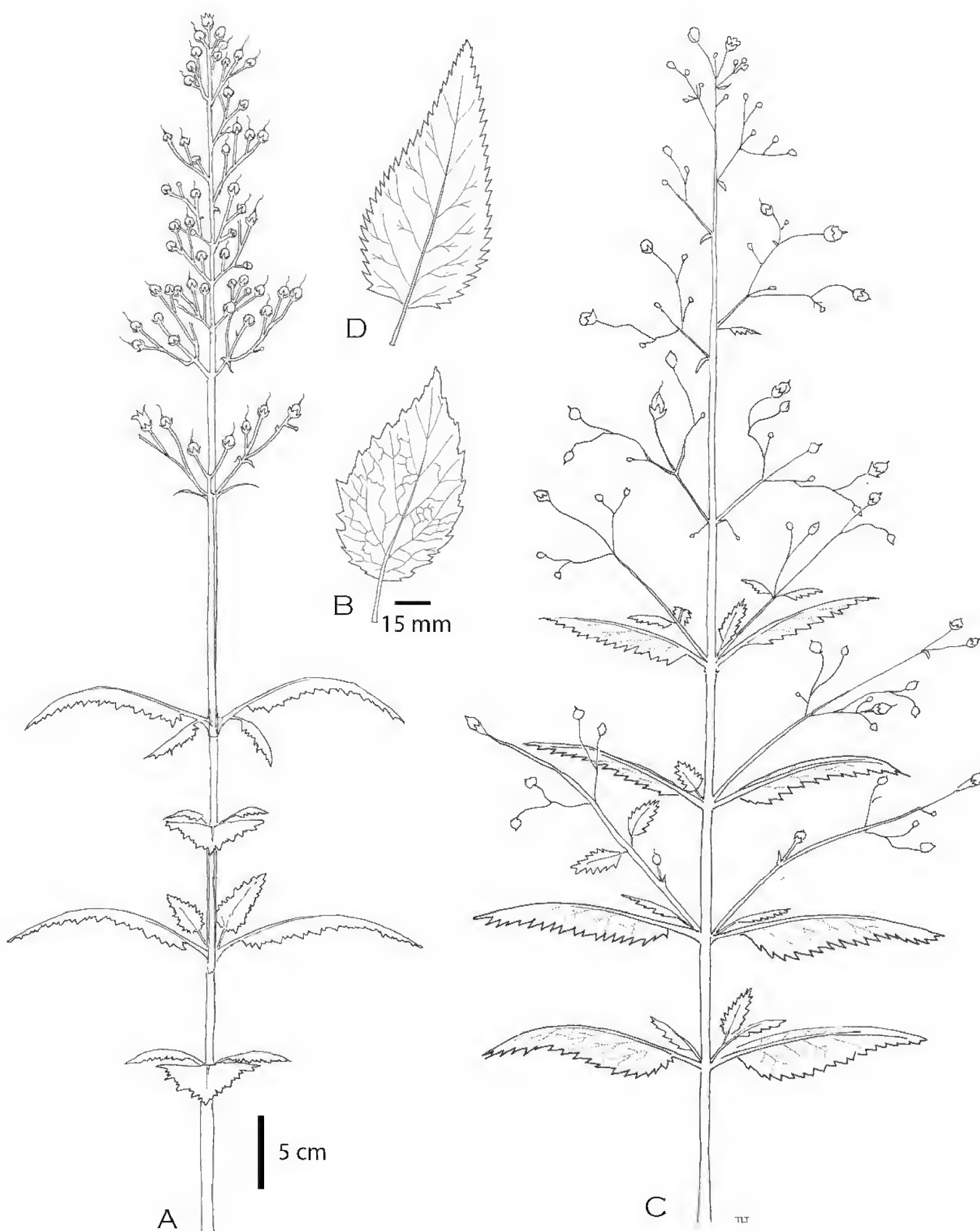


**Scrophulariaceae** Figure 2. Distribution of: (A) *Verbascum thapsus*; (B) *V. virgatum*.

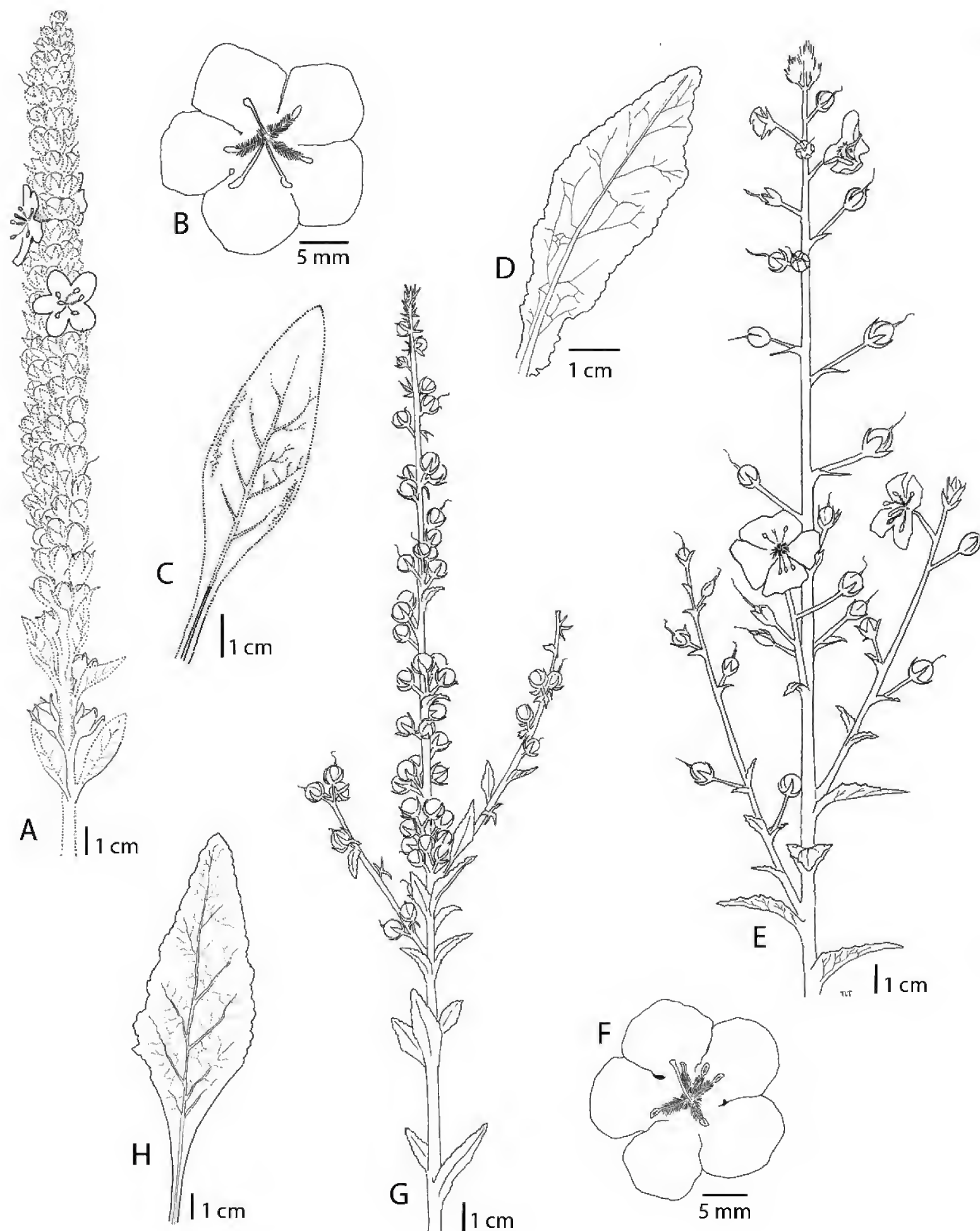


**Scrophulariaceae** Figure 3. *Limosella*. (A-B) *L. aquatica*; (A) habit; (B) flower; (C) *L. acaulis* flower. Illustration by Tracy Tohanne.



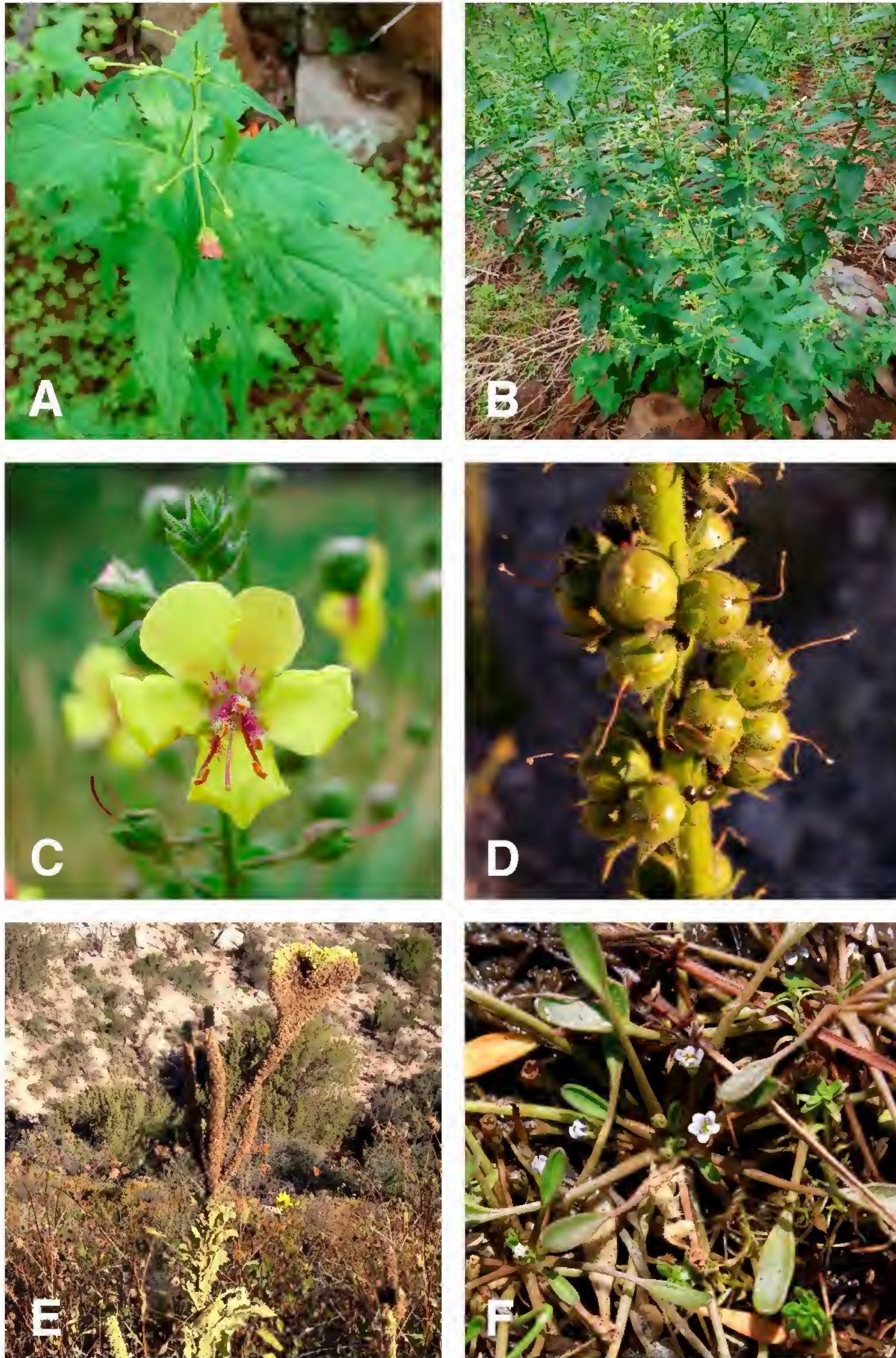


**Scrophulariaceae** Figure 4. *Scrophularia*. (A-B) *S. lanceolata*; (A) inflorescence; (B) leaf; (C-D) *S. parviflora*; (C) inflorescence; (D) leaf. Illustration by Tracy Tohanne.



**Scrophulariaceae** Figure 5. *Verbascum*. (A-C) *V. thapsus*; (A) inflorescence; (B) flower; (C) basal leaf; (D-E) *V. blattaria*; (D) basal leaf; (E) inflorescence; (F-H) *V. virgatum*; (F) flower; (G) inflorescence; (H) basal leaf. Illustration by Tracy Tohanne.





**Scrophulariaceae** Figure 6. (A-B) *Scrophularia parviflora*; (C) *Verbascum blattaria*; (D) *Verbascum virgatum*; (E) *Verbascum thapsus* with a fasciated inflorescence; (F) *Limosella pubiflora*. Photos A-D by Max Licher; E by Kate Noonan; F by Steve Buckley.



## SOLANACEAE Part Six: NICOTIANA L. Tobacco

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Annuals to soft-woody trees and shrubs. Herbage glabrous to viscid-glandular. LEAVES simple, alternate, petioled, sessile, or clasping; margins entire, often with some degree of progressive change in leaf shape and petiolation from base to inflorescence. INFLORESCENCES generally terminal panicles with varying degrees of complexity, sometimes raceme-like. FLOWERS synsepalous, sympetalous, actinomorphic or nearly so, tubular to salverform, the calyx commonly much shorter than the tube, the lobes equal or unequal in length; corollas white to pale green or yellow, the tube-proper cylindrical to subcylindrical, often with various forms of bulging or dilation; limb subentire to deeply 5-lobed; stamens 5, included or nearly so, the filaments inserted on corolla at various points, commonly below the middle of the tube. FRUITS apically dehiscent capsules, slightly woody in ours. SEEDS numerous, angular, globose or reniform, 0.4–1.3 mm long, surfaces with various ridges and patterns.— Ca. 65 spp. native to w hemisphere, Australia, and a few s Pacific islands; widely naturalized and cultivated. (For Jean Nicot, 1530–1604, French ambassador, diplomat, explorer). *Nicotiana tabacum* L. grown worldwide for tobacco products.

*Nicotiana attenuata*, *N. clevelandii*, *N. quadrivalvis*, and *N. sylvestris* are vespertine species and consideration should be taken when keying out herbarium material and/or specimens collected later in the day since measurements of floral characters such as limb shape, orientation, and lobe length can be obscured as flowers begin to close.

1. Shrub or small tree; herbage glabrous, glaucous; flowers yellow; pedicels strongly recurved in fruit.....*N. glauca*
- 1' Annuals to suffrutescent herbs; herbage glandular-hairy; flowers white, cream, pale green, sometimes pale purple, not yellow; pedicels not strongly recurved in fruit.
  2. Perennial herbs to 2 m tall; basal leaves clasping, 30–50 cm long; flowers in congested panicles, drooping downward; corolla slightly dilated along upper ½ of tube.....*N. sylvestris*
  - 2' Annual to suffrutescent perennial herbs, usually much less than 2 m tall; basal leaves clasping or petioled, less than 30 cm long; flowers in more or less open panicles, upright or nodding, not drooping downward; corolla tube not noticeably dilated.
    3. Herbaceous perennial, often suffrutescent; cauline leaves often clasping; flowers diurnal; calyx 1/3–3/4 the length of the corolla tube .....*N. obtusifolia*
    - 3' Annual or short-lived perennial herbs; cauline leaves not clasping (except in *N. quadrivalvis*); flowers vespertine; calyx less than ½ the length of the corolla tube.
      4. Plants ill scented; cauline leaves usually clasping (sometimes only slightly so); corolla in longest flowers 35–70 mm long; stamens attached above the middle of the tube. .... *N. quadrivalvis*

- 4' Plants not ill-scented; cauline leaves never clasping; corolla in longest flowers 20–33 mm long; stamens attached below the middle of the tube.
5. Calyx lobes unequal with one longer than the other four; capsule shorter than longest calyx lobes; cauline leaves sessile to subsessile; plants of lower elevations in sandy soils in sw AZ. .... *N. clevelandii*
- 5' Calyx lobes not markedly unequal; capsule protruding beyond the calyx lobes; cauline leaves petiolate; plants in mid and higher elevations in various habitats throughout AZ, except extreme sw AZ. .... *N. attenuata*

*Nicotiana attenuata* Torr. ex S. Wats. (for attenuate leaves). Coyote Tobacco.—Erect annuals or short-lived perennials, occasionally over 1 m tall, the stems with glandular hairs. LEAVES elliptic to lanceolate, the blades 6–15 cm long, 1–4 cm wide; cauline leaves reduced distally becoming narrowly lanceolate to linear; petioles diminishing distally; basal leaves rosette forming, especially when young. INFLORESCENCES racemose. FLOWERS vespertine; calyx 5–9 mm long, the lobes subequal; corolla salverform, white to pale green, the tube-proper often flushed with purple; corolla (25–)28–35(–40) mm long; lobes obtuse; stamens unequal, attached below the middle of the tube. FRUITS ovoid, 8–15 mm long, protruding beyond the calyx lobes. SEEDS more or less reniform, surfaces with irregular, sinuous ridges.—Alluvial soils in washes and disturbed sites, occasional on flats, and slopes: Apache, Cochise, Coconino, Gila, Graham, Maricopa, Mohave, Navajo, Pima, Pinal, and Yavapai cos.; 300–2600 m (1000–8500 ft); flowering Apr–Oct; CA, CO, ID, MO, NM, NV, OR, UT, WA, WY, w Can., Mex. There are three historical records out of the otherwise known range for this species: Pima County, “Tucson, Ariz.” *J. W. Toumey s.n.*, 9/14/1891 (ARIZ); Pinal County, “River bottom near Sacaton” *G. J. Harrison 1962*, 5/29/1926 (ARIZ), and Maricopa County, “Agua Fria river bottom near Avondale P. O.” *G. J. Harrison 1817*, 5/9/1926 (ARIZ).

*Nicotiana attenuata* differs most obviously from the similar species *N. clevelandii* in its petiolate cauline leaves and exserted capsule.

*Nicotiana clevelandii* A. Gray (for Daniel Cleveland, 19<sup>th</sup> century botanist). Cleveland's Tobacco.—Erect annuals usually less than 1 m tall; stems with glandular hairs. LEAVES elliptic to oblanceolate to lanceolate, the blades 2–12 cm long, 1–4 cm wide; cauline leaves subsessile to sessile, reduced distally; basal leaves petiolate and rosette forming. INFLORESCENCES racemose, sometimes branched into a panicle-like habit. FLOWERS vespertine; calyx 7–12 mm long; calyx lobes unequal with one longer than the 4 others; corolla white-cream to pale green, often with violet flush along the tube, 15–30 mm long; limb slightly zygomorphic, with shallow triangular lobes, these with rounded edges and acute tips, 1–3 mm long. Stamens unequal, attached below the middle of the tube. FRUITS: capsules shorter than the calyx lobes, ovate-elliptic, 7–10 mm long. SEEDS more or less reniform, the surfaces with irregular, sinuous ridges.—Dunes, washes, and other well-drained, sites, occasional on flats and slopes: sw Arizona in Maricopa, Pima and Yuma cos.; to 800 m (to 2600 ft); flowering Jan–May; s CA; Baja C., Mex. and w Son., Mex.

*Nicotiana clevelandii* differs most obviously from the similar species *N. attenuata* in its sessile to subsessile cauline leaves and the included capsule.



***Nicotiana glauca*** Graham (bluish, waxy surface). Tree Tobacco.—Soft-woody, loosely branched shrub to small tree; young stems greenish or bluish-grey, glabrous and glaucous. LEAVES relatively thick, rubbery, glaucous, the blades elliptic to ovate, often with oblique bases, 1–10 cm long, 1–8 cm wide (measurements are from blade portion of the leaf, not the petiole, and from herbarium material which rarely includes basal leaves), reduced distally; petiole sometimes equal to the length of the blade. INFLORESCENCES congested panicles. FLOWERS diurnal; calyx 8–12 mm long, the lobes equal, triangular, narrowing to somewhat linear tips, 1–3 mm long, three to five times shorter than calyx tube; corolla tubular, the apical portion bulging slightly, then constricted, bright yellow to greenish yellow, 2–4.5 cm long; limb pentagonal with inconspicuous lobes ~1 mm long. FRUITS ovoid or broadly ellipsoid, 7–10 mm long, borne on strongly recurved pedicels so fruit opening is directed upward at maturity. SEEDS slightly longer than wide, angular to oval with irregular, sinuous ridges.—Riparian areas, well-drained rocky to sandy soils in washes, and disturbed sites with moisture. Cochise, Gila, Graham, Greenlee, Maricopa, Mohave, Pima, Pinal, Santa Cruz, Yavapai, and Yuma cos.; to 2500 m (to 7500 ft); flowering throughout the year; AL, CA, LA, MS, NM, TX, s UT; Mex, S. Amer.

***Nicotiana obtusifolia*** M. Martens & Galeotti (blunt or rounded leaf apex). Desert Tobacco.—Perennial herbs suffrutescent with age, to 1.5 m tall; herbage with glandular hairs, many are multicellular and branched. LEAVES mostly oblanceolate, 2–20 cm long; cauline leaves sessile and usually clasping with auriculate bases, reduced distally; basal leaves petiolate, not usually rosette forming. INFLORESCENCES panicle-like, the peduncles secund. FLOWERS diurnal; calyx 8–14 mm long, 1/3 to 3/4 as long as the corolla tube; corolla tubular, with reflexed lobes, subsalverform; pale green to whitish, 17–27 mm long; limb circular-pentagonal with broadly triangular lobes; filaments attached to corolla near base. FRUITS ovoid, 8–12 mm long. SEEDS oval to subreniform to angular, the surfaces alveolate to irregularly ridged. [*N. trigonophylla* Dunal].—Well-drained rocky to sandy soils in washes and disturbed sites, occasional on flats and slopes; all counties in AZ; to 1800 m (to 6000 ft); flowering throughout the year; CA, NM, s NV, w TX, s UT; Mex.

***Nicotiana quadrivalvis*** Pursh (four valves). Indian Tobacco.—Annual or short-lived perennial to 1.5 m tall, ill scented; stems with glandular hairs. LEAVES oblanceolate to lanceolate, 3–12 cm long, 1–4 cm wide; cauline blades sessile to subsessile, usually slightly clasping, becoming shorter and narrower distally; basal leaves petiolate, rosette forming. INFLORESCENCES usually racemose, occasionally with dichotomous branching near the apex. FLOWERS vespertine, closing by midday; calyx 12–20 mm long, the lobes often unequal in length; corolla trumpet-shaped (funnel-form-salverform), 35–70 mm long, throat elongate, outer surface pale green to white, sometimes with slight violet flush along lower portion of limb; limb 5–20 mm long, conspicuously cleft into triangular lobes; stamens unequal; filaments attached at different levels above middle of tube. FRUITS narrowly ovoid to globose, 10–18 mm long. SEEDS oval-reniform, with irregular, sinuous ridges. [*Nicotiana bigelovii* var. *quadrivalvis* (Pursh) Eastw.].—Alluvial sandy soils in washes and disturbed sites, occasional on flats, and slopes; Maricopa, Mohave, and Yavapai cos.; to 1600 m (to 5200 ft); flowering Apr–Nov; s CA; Baja C., Mex., w Son., Mex. *Nicotiana quadrivalvis* has been collected 6 times in Arizona – 5 times in the Hassayampa River watershed and once in the Burro Creek watershed.



*Nicotiana quadrivalvis* differs most obviously from the similar species *N. attenuata* and *N. clevelandii* in its robust flowers with longer tube, much wider limb and longer corolla lobes.

***Nicotiana sylvestris*** Spegazzini & Comes (of the forest). Woodland Tobacco, South American Tobacco.—Annual, biennial, or perennial to 2 m tall, glandular hairy. LEAVES elliptic-ovate, to approximately 50 cm long and 30 cm wide; cauline leaves reduced distally, elliptic-ovate and auriculate-clasping, the uppermost becoming ovate-triangular with acuminate apices; basal leaves auriculate-clasping, usually rosette forming. INFLORESCENCES congested panicles, sometimes described as glomerulate. FLOWERS verspertine, drooping downward, the pedicels to 25 mm at maturity; calyx 10–15 mm long, the lobes equal or nearly so. Corolla white, salverform, 6–10 cm long exclusive of limb; upper ½ of tube slightly dilated; limb 10–15 mm long, with broadly triangular to acute lobes; stamens unequal; filaments attached below middle of tube. FRUITS oval or ovoid, 15–18 mm long. SEEDS oval-subreniform, dull, surfaces with irregular, sinuous ridges.—Riparian and residential areas; Santa Cruz and Cochise cos.; 1000–1500 m (3,500–5,000 ft); flowering Aug.

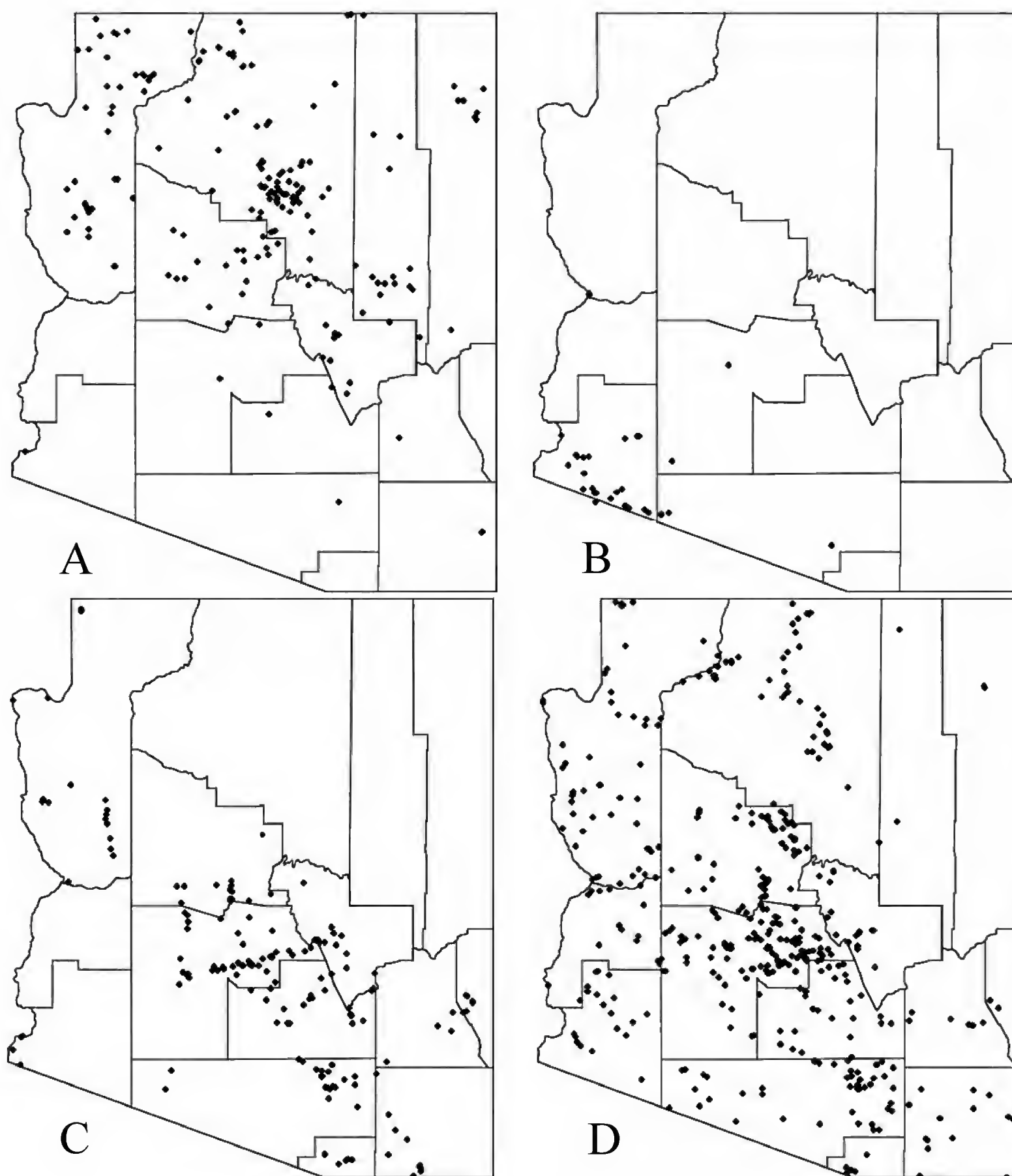
*Nicotiana sylvestris* is native to South America and cultivated as an ornamental throughout the US. It has occasionally escaped cultivation and has been collected twice in AZ: Santa Cruz County, Patagonia Lake along Sonoita Creek (*T. R. VanDevender & A. L. Reina G. 2010-840*) in 2010 (ARIZ, ASU); Cochise County, Chiricahua National Monument residential area (*T. Reeves R-4050*) in 1975 (ASU). The Cochise County plant(s) is no longer there. A third locality was confirmed from a photo taken by Craig Riedl taken on 24 November 2016, also along Sonoita Creek, just upstream from Patagonia Lake. A visit to this locality is needed to collect a voucher specimen.

#### ACKNOWLEDGEMENTS

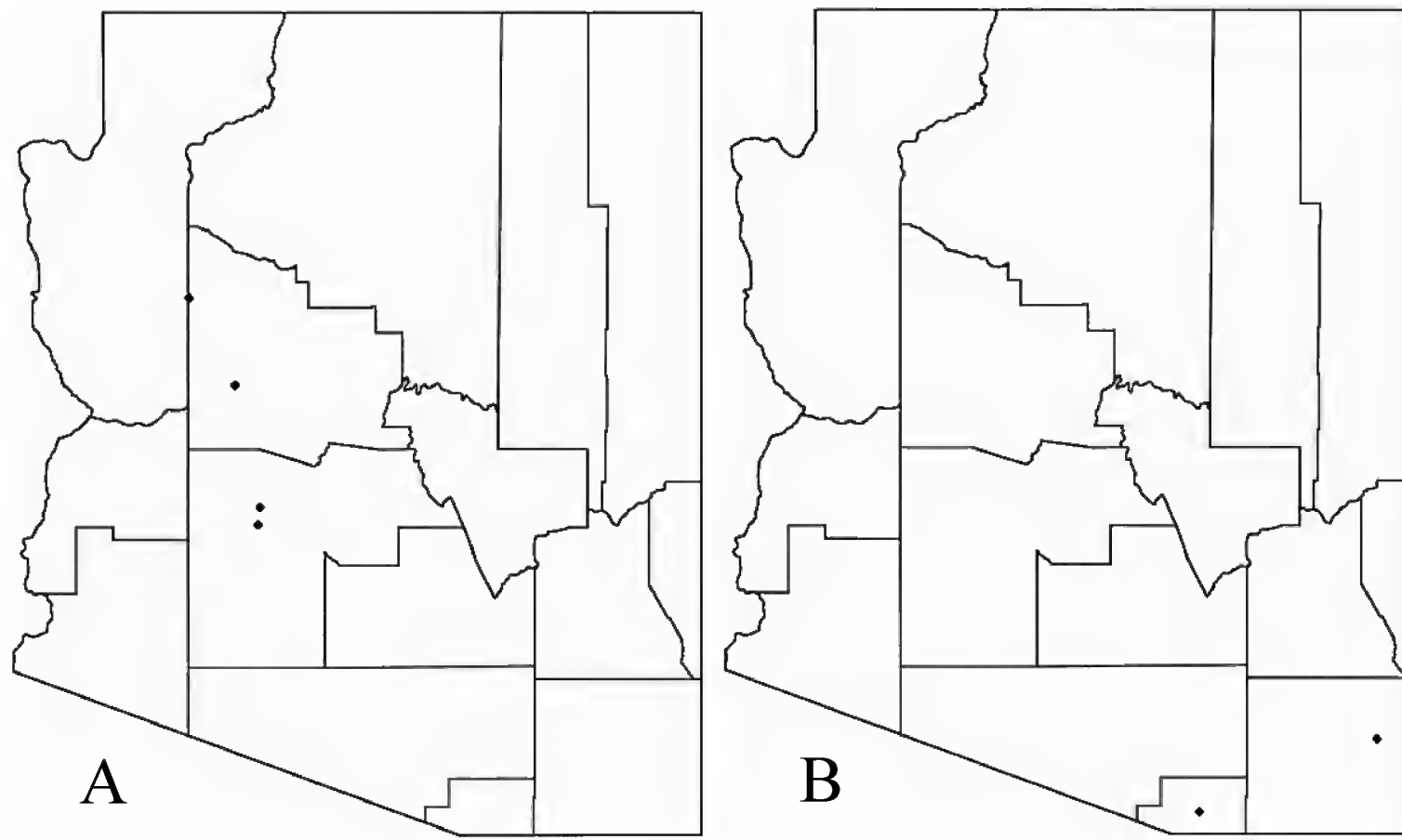
We thank the Rancho Santa Botanic Garden Herbarium (RSA) for their generous loan of specimens, and the University of Arizona Herbarium for making their specimens available. Maps were made using Daryl Lafferty's program [<http://symbiota4.acis.ufl.edu/dlafferty/PlantMap/>] using the specimen data available on SEINet [<http://swbiodiversity.org/seinet/index.php>].

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- HICKMAN, J. C., editor. 1993. *The Jepson Manual: Higher Plants of California*. University of California Press, Berkeley and Los Angeles, California.



**Solanaceae: *Nicotiana*.** Figure 1. Distributions. (A) *N. attenuata*; (B) *N. clelandii*; (C) *N. glauca*; (D) *N. obtusifolia*.



**Solanaceae: *Nicotiana*.** Figure 2. Distributions. (A) *N. quadrivalvis*; (B) *N. sylvestris*.



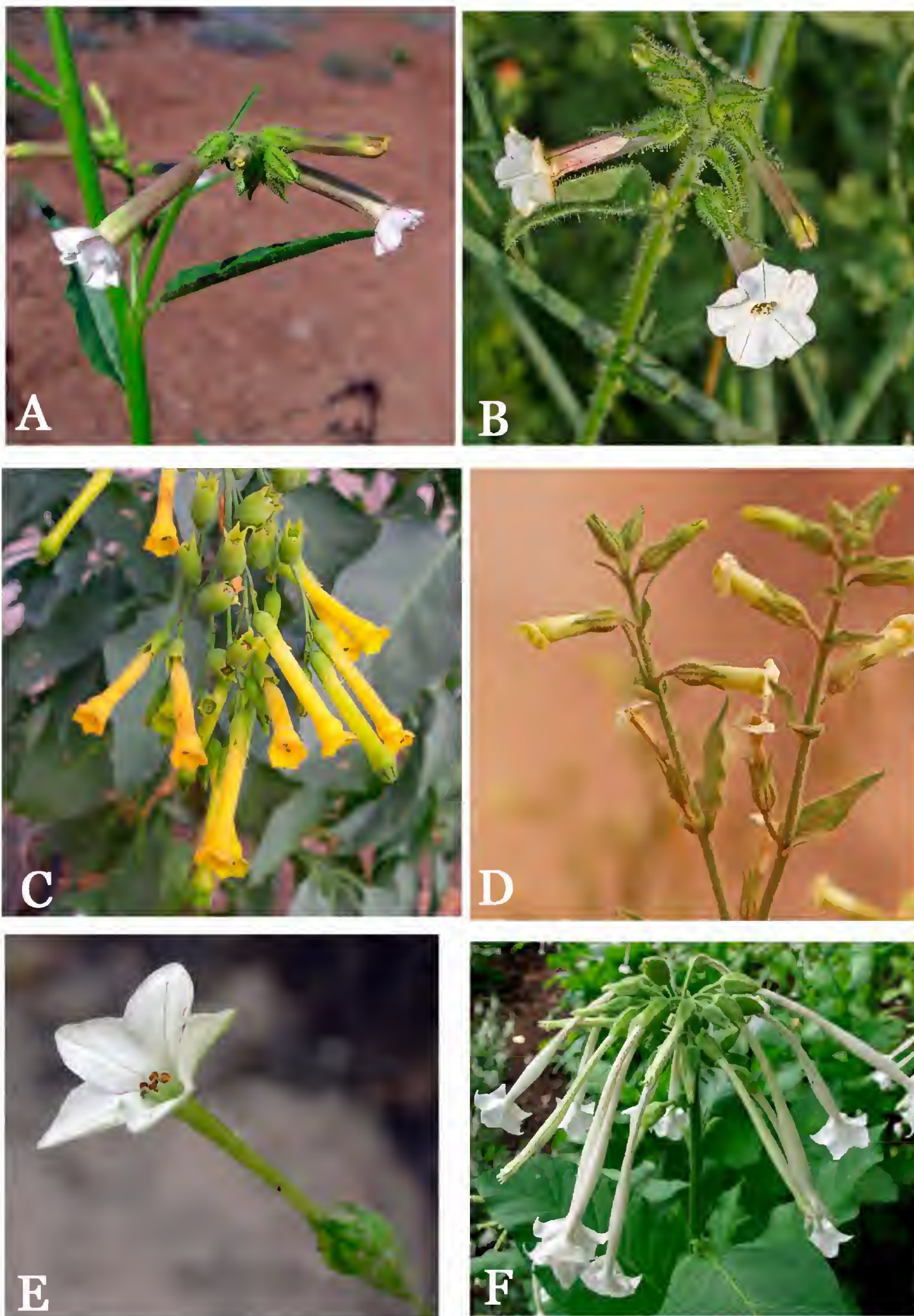


**Solanaceae: *Nicotiana*.** Figure 3. (A) *N. attenuata*; (B) *N. clevelandii*; (C) *N. glauca*; (D) *N. obtusifolia*. Drawings by M. Blos from Goodspeed (1954).



**Solanaceae: *Nicotiana*.** Figure 4. (A) *N. quadrivalvis*; (B) *N. sylvestris*. Drawings by M. Blos from Goodspeed (1954).





**Solanaceae: *Nicotiana*.** Figure 5. (A) *N. attenuata*, (B) *N. clevelandii*; (C) *N. glauca*; (D) *N. obtusifolia*, (E) *N. quadrivalvis*, (F) *N. sylvestris* Photo credits: A,C, by Max Licher; B,D by Elizabeth Makings; E by Keir Morse; F courtesy of Longwood Gardens, Kennett Square, PA [<https://longwoodgardens.org/>].



## ZANNICHELLIACEAE

## HORNED PONDWEED FAMILY

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Submerged aquatic herbs, primarily annuals, dioecious or monoecious. STEMS caulescent. LEAVES opposite, alternate and/or pseudowhorled on the same plant, linear, sessile, the stipules forming a hyaline tubular sheath, non-persistent, the sheath usually ligulate at the apex. INFLORESCENCES solitary or cymose, axillary. FLOWERS unisexual, sessile; perianth generally absent; staminate flowers often with 3 minute transparent scales, with 1–3 stamens, the filaments slender, the anthers 1–4-celled, dehiscing longitudinally; pistillate flowers with 1 to 9 pistils, the styles short to long, the stigmas capitate to peltate, or 2–4-lobed; ovules solitary, pendulous. FRUITS drupaceous, 1-seeded, indehiscent, sessile or generally on a short stipe.—4 genera, 10–12 spp., nearly worldwide. Haynes, R. R. & C. B. Hellquist. 2000. Zannichelliaceae. *in* Flora of North America. 22: 84–85.

### **Zannichellia** L.

### Horned Pondweed

LEAVES entire, 1–3-veined, generally terete. INFLORESCENCES axillary, usually 2-flowered cymes of a single staminate and pistillate flower, usually enclosed in bud by a non-persistent sheath. STAMINATE FLOWERS usually solitary; stamen usually 1, the filament usually long and slender, exceeding the pistillate flower, the anthers 4-celled. PISTILLATE FLOWERS enclosed in a non-persistent membranaceous, hyaline sheath; pistils 2 to 8, the styles short, persistent in fruit, the stigmas peltate, asymmetrical. FRUITS obliquely oblong (slightly incurved), laterally compressed, usually minutely to deeply dentate on the convex margin, rarely smooth; endosperm often coarsely papillose; developing fruits usually on a short stipe.—4–5 spp., nearly worldwide. (named in honor of Gian Girolamo Zannichelli, 1662–1729, a Venetian apothecary and botanist).

**Zannichellia palustris** L. (marshy, swampy). Common Poolmat.—Annual, monoecious, rooted on the bottom and generally floating below the surface of the water. STEMS simple to much-branched, generally slender, to 50 cm long, 0.2–0.6 mm thick. LEAVES linear to filiform, 2–10 cm long, 0.2–1 mm wide, sessile, the apex acute, often sharply pointed, generally 1-nerved; sheath membranaceous, scarious, 0.2–2 cm long. STAMINATE FLOWERS with filaments 1.5–2 mm long, the connective with a prolonged blunt tip 0.1 mm long. PISTILLATE FLOWERS sessile at first, often on a short stipe after anthesis; pistils 2 to 8, the styles recurved, persistent, 0.4–0.7 mm long. FRUITS 1.7–2.8 long, 0.6–0.9 mm wide, the rostrum 0.7–2 mm long, the stipe 0.1–1.5 mm long.  $2n = 12, 24, 28, 32, 36$ .—Slow moving streams, lakes, ponds, tanks: all cos. (Fig. 1); 300–1700 m (900–5500 ft.); flowering and fruiting summer and fall; throughout N. Amer., C. Amer., S. Amer., W. Indies, Africa, Eurasia and Australia.

The architecture of the ribbing of the fruit can vary greatly, from nearly smooth to excessively spiny, although the “banana-like” shape of the fruit generally remains constant. The

genus *Zannichellia* is in need of global revision, the identity of non-European, especially North American species are generally considered to be *Z. palustris* L.

### LITERATURE CITED

HAYNES, R. R. AND C. B. HELLQUIST. 2000. Zannichelliaceae. Pp. 84–85. *In*: Flora of North America Editorial Committee (eds.). *Flora of North America north of Mexico*. Vol. 22. New York: Oxford University Press.

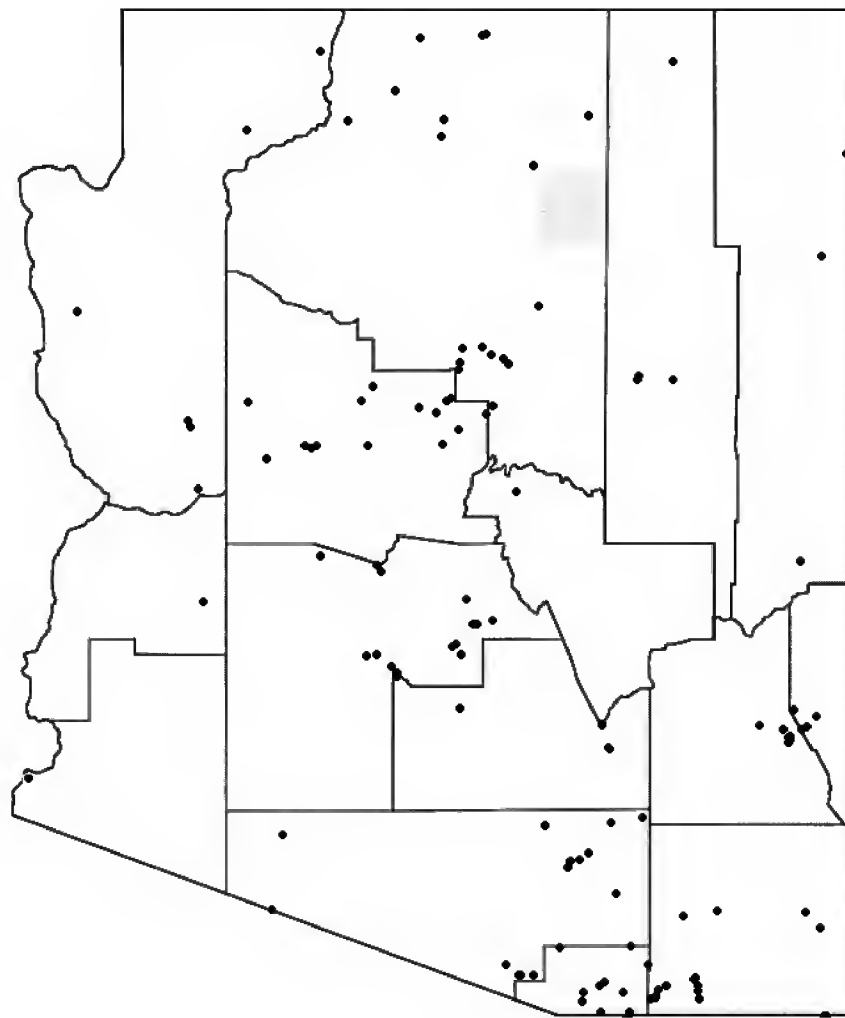


Figure 1. Distribution Map of *Zannichellia palustris*.

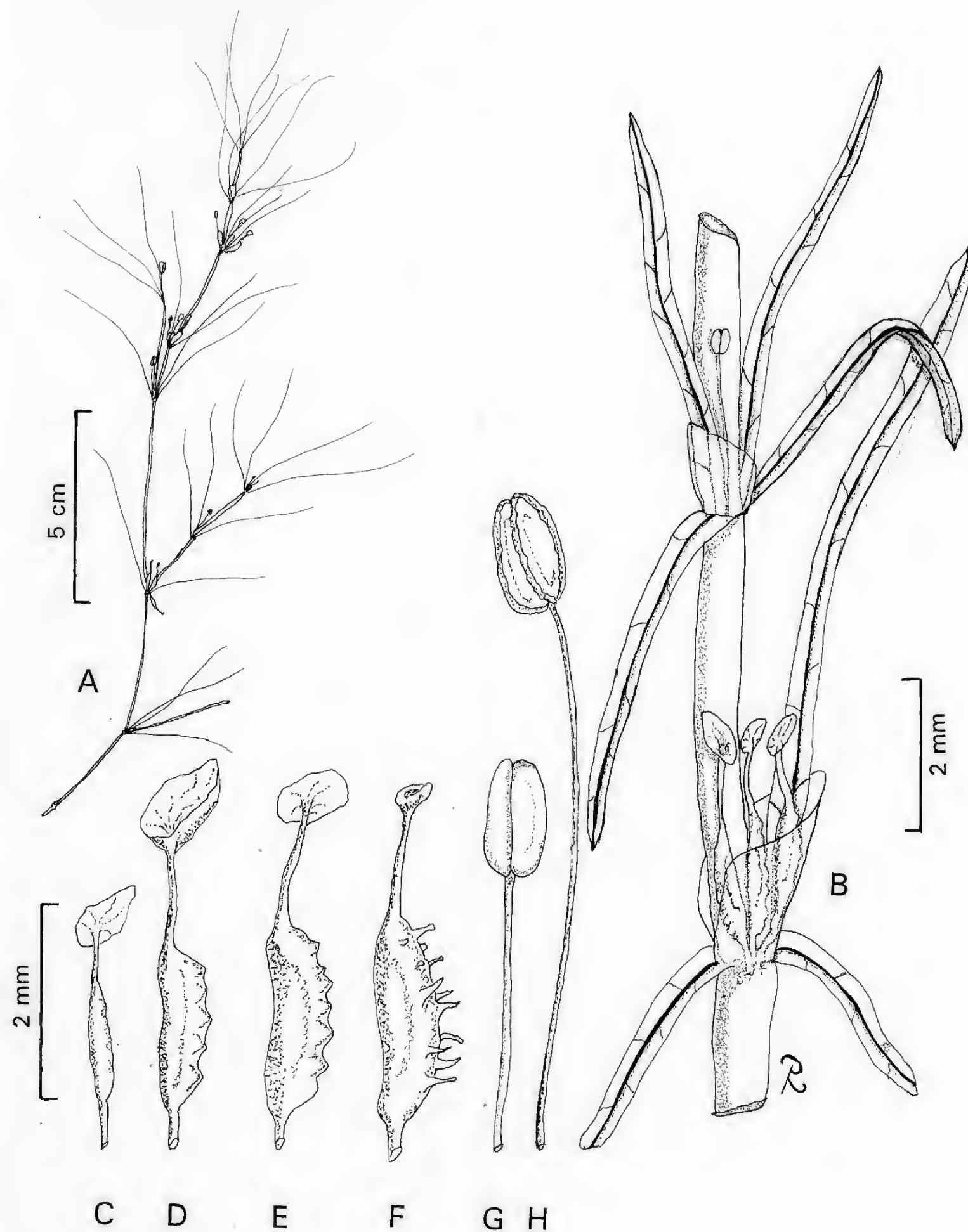


Figure 1. *Zannichellia palustris* L. A. Habit. B. Detail of stem showing a staminate and pistillate inflorescence. C–F. Maturing pistil showing degrading stigma and development of “spines”. G–H. Maturing stamen showing filament growth and anther dehiscence at anthesis. [Drawn by Jon Ricketson].



# Analysis of infraspecific taxa within *Cylindropuntia acanthocarpa* using multivariate analysis of morphological characters

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**ABSTRACT:** The circumscription of infraspecific taxa of *Cylindropuntia acanthocarpa* was evaluated using multivariate analysis of morphological characters, with *C. echinocarpa* as the outgroup. Our primary objectives were to sample and analyze sufficient morphological data to determine: 1) how populations within *C. acanthocarpa* might be best grouped, 2) whether means for certain character values differ significantly among groups, and 3) whether these groups of populations correlate with geography and/or habitat type. A review of the literature indicated that the basionym *Opuntia acanthocarpa* var. *major* was incorrectly interpreted by L. Benson and that southeastern populations of *C. acanthocarpa* should instead fall under the name *C. acanthocarpa* var. *ramosa*. Our analyses did not support the recognition of *C. acanthocarpa* var. *coloradensis* as a separate taxon from *C. acanthocarpa* var. *acanthocarpa* but supported the recognition of *C. acanthocarpa* var. *thornberi*. Although individuals of *C. acanthocarpa* var. *ramosa* were more weakly defined, their morphology was correlated with geography, and therefore the name retains some usefulness and should be maintained. A new neotype is selected for *Opuntia echinocarpa* var. *major*, and a lectotype is designated for *O. acanthocarpa* var. *ramosa*.

## INTRODUCTION

Six basionyms have been published for the *Cylindropuntia acanthocarpa* complex and two for *C. echinocarpa* as they are presently circumscribed, and several new combinations within both species have been proposed. The limits of infraspecific taxa within *C. acanthocarpa* have not been clear, and it has been the purpose of this morphometric study to clarify these limits as much as possible. The nomenclature of

this group is complex and often confusing. We believe that mistakes have been made in the past, and we try to correct some of these in the nomenclature discussion following the morphometric analysis.

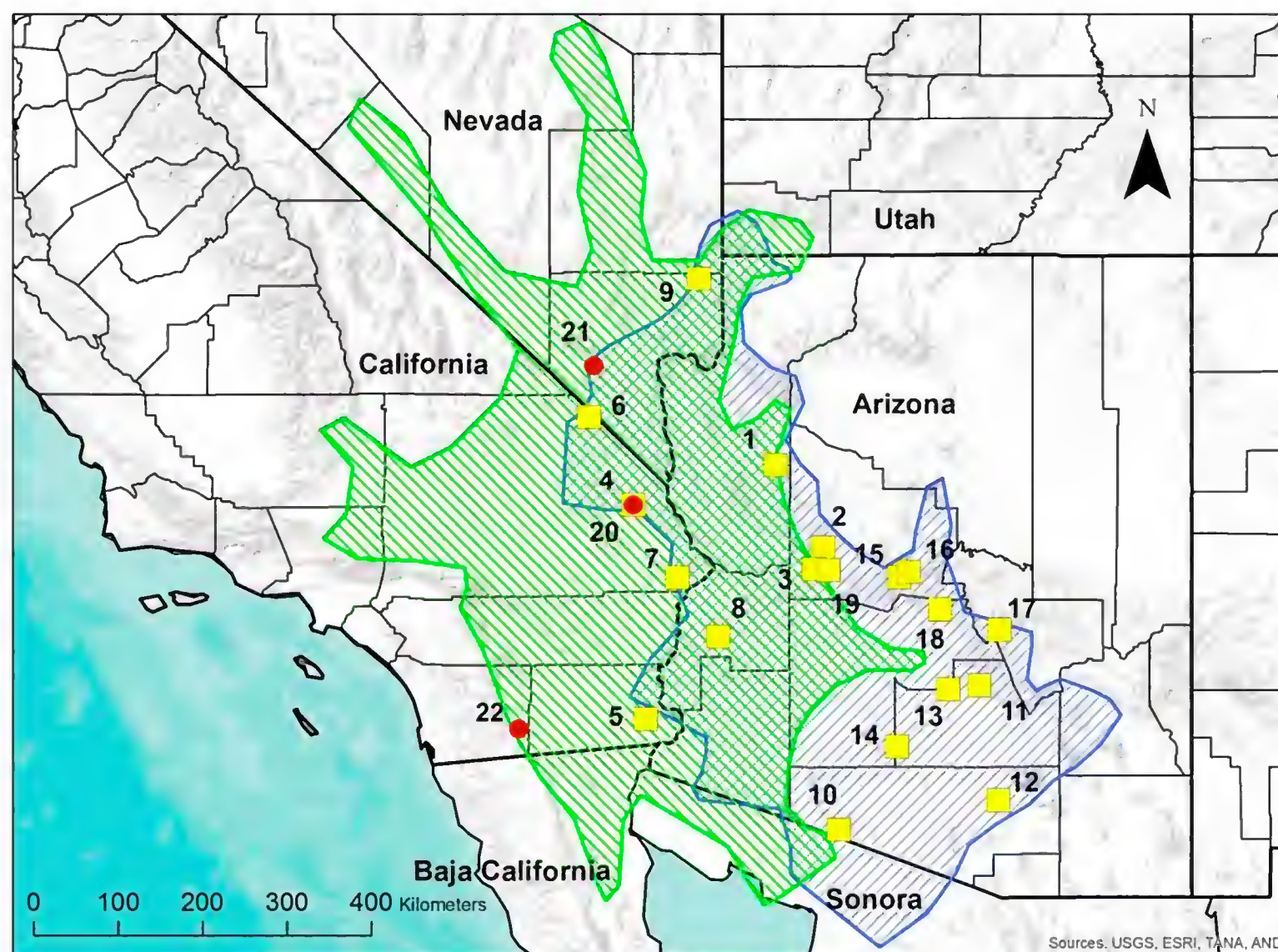
Most recent treatments have divided *Cylindropuntia acanthocarpa* into four varieties: *C. acanthocarpa* var. *acanthocarpa*, *C. acanthocarpa* var. *coloradensis*, *C. acanthocarpa* var. *major*, and *C. acanthocarpa* var. *thornberi* (Benson 1982, Pinkava 2003). Distinguishing among these varieties is ambiguous because of a large degree of morphological variability within and among populations and because some type localities occur within areas of morphological intermediacy between two varieties. These problems have been exacerbated by an injudicious choice of neotypes. The extent of this taxonomic confusion is readily apparent from an herbarium database search of the Southwestern Environmental Information Network (SEINet 2014). Of 758 georeferenced *C. acanthocarpa* specimens, only 173 (22.8%) are identified to the variety or subspecies level. Guzmán et al. (2003) made numerous recombinations in the Cactaceae, primarily changing varieties to subspecies, with little explanation. Although we have no strong opinions regarding the use of variety versus subspecies, we treat infraspecific taxa within *C. acanthocarpa* as varieties, which is traditional for the genus.

In order to apply the names correctly, it is necessary to circumscribe recognizable entities, and that has been the purpose of this morphometric analysis. We evaluated morphological characters for populations of *Cylindropuntia acanthocarpa* throughout its range and for selected populations of the outgroup, *C. echinocarpa*. *Cylindropuntia echinocarpa* was selected as an outgroup because it is morphologically similar to and often sympatric with *C. acanthocarpa*, though there is no assumption of close evolutionary relatedness. Chromosome number determinations of  $n = 11$  (diploid) have been made numerous times for both species, including those at all of the type localities (Baker et al. 2009; Pinkava et al. 1985, 1992, 1998). Our primary objectives were 1) to sample and analyze sufficient morphological data to define how populations within *C. acanthocarpa* are best grouped, 2) to discover whether means for certain character values differ significantly among groups, and 3) to discover whether these groups of populations correlate with geography and/or habitat type.

## METHODS

Twenty-two populations were sampled, 19 for *Cylindropuntia acanthocarpa* and three for the outgroup, *C. echinocarpa*. Populations were chosen from across the ranges of the species and included type localities. An attempt was made to sample at least 30 individuals within each population. A total of 571 individuals were sampled for *C. acanthocarpa* and 89 for *C. echinocarpa* (Figure 1, Table 1). Characters measured are presented in Table 2. Except for individual height and width, each character was measured three times from separate areas on the trunk or from separate stems. Plant height and width were not used for the multivariate analyses because, although useful for taxonomic descriptions, values for these characters are age-dependent. Statistical analyses were performed using SPSS 22® (IBM 2013).





**Figure 1.** Locations of populations sampled for the morphological analysis of *Cylindropuntia acanthocarpa* and *C. echinocarpa*. Note that populations 4 and 20 occur in the same locality and represent the type locality for *C. acanthocarpa* var. *coloradensis* (as *Opuntia acanthocarpa* var. *coloradensis*) and the neotype locality for *C. echinocarpa* (as *O. echinocarpa*), respectively. Yellow squares = *C. acanthocarpa*, red circles = *C. echinocarpa*. Green hash-marks = known distribution of *C. echinocarpa*, blue hash-marks = known distribution of *C. acanthocarpa*.

For our initial analysis, discriminant function analysis (DFA) was used to place clusters of populations with morphological affinities into potential taxonomic groups (PTGs) by defining population as the dependent (grouping) variable (Tabachnick & Fidell 1996). We chose populations that appeared to be morphologically uniform in that there was no apparent hybridization and assumed that all individuals within each population site were of the same taxon. The one exception to this rule was the site from which both the holotype of *Opuntia acanthocarpa* var. *coloradensis* and the neotype for *O. echinocarpa* had been collected by L. Benson. At this site, individuals were selected as representatives of either taxon based on their general morphology, including habit. Potential taxonomic groupings of populations were then chosen by the proximity of their centroids (Figure 2) and to a lesser extent by the proximity of their geographical distribution. Iterations of DFA were then used to compare the significance of various taxonomic arrangements. Once the PTG with the highest percent of correct classification of individuals was ascertained, multiple analyses of variance (MANOVA) were used to



determine which characters were significantly different among the newly-defined taxonomic grouping.

**Table 1.** Locations, sample sizes, and herbarium vouchers of populations sampled for the morphological analysis of *Cylindropuntia acanthocarpa*.

Site no.	Taxon	Locality	N	Latitude, longitude	Elev. (m)	Voucher(s) collector and number
1	<i>C. acanthocarpa</i>	Arizona, Mohave County, vicinity of Cactus Pass, 50 km east of Kingman; <b>type locality for <i>Opuntia acanthocarpa</i></b>	30	35.1880° -113.4779°	1465	MAB 11813 (ASU)
2	<i>C. acanthocarpa</i>	Arizona, Yavapai County, McCloud Mountains, 5.5 km WNW of Hillside, <b>near neotype locality for <i>Opuntia acanthocarpa</i></b>	31	34.4664° -112.9684°	1110	MAB 17671 (ASU), L. Benson 10874 (RSA, ARIZ, CAS)
3	<i>C. acanthocarpa</i>	Arizona, Yavapai County, 17.5 km SE of the summit of Ives Peak, 2 km north of Date Creek, just west of the Date Creek Mountains, 65 km SW of Prescott	30	34.2771° -113.0710°	887	MAB 17673 (ASU)
4	<i>C. acanthocarpa</i>	California, San Bernardino County, 9 km WSW of South Pass, 32 km due west of Needles, just south of Interstate 40, <b>type locality for <i>Opuntia acanthocarpa</i> var. <i>coloradensis</i></b>	30	34.8375° -114.9848°	670	L. Benson 10375 (RSA, ARIZ) Baker 16724.1 (ASU)
5	<i>C. acanthocarpa</i>	California, Imperial County, 5 km NW of the north end of the Cargo Muchacho Mountains, 32 km NW of Yuma, Arizona	30	32.9452° -114.8558°	190	MAB 17541.1 (ASU)
6	<i>C. acanthocarpa</i>	California, San Bernardino County, Ivanpah Valley, 13 km NNE of the summit of Clark Mountain, 67 km SE of central Las Vegas	30	35.6040° -115.4600°	900	MAB 17660 (ASU)
7	<i>C. acanthocarpa</i>	California, San Bernardino County, 5 km ENE of Vidal Junction, 8 km south of Savahia Peak, lower bajada to the SW of the Whipple Mountains	30	34.1994° -114.5216°	295	MAB 17718 (ASU, RSA)
8	<i>C. acanthocarpa</i>	Arizona, La Paz County, Plomosa Mountains, 13 km east of Quartzsite	30	33.6821° -114.0865°	440	MAB 17718 (ASU, RSA)
9	<i>C. acanthocarpa</i>	Nevada, Clark County, Mormon Mesa, 103 km NE of central Las Vegas	30	36.7993° -114.2928°	655	MAB 18670, 18671 (ASU, UNLV)
10	<i>C. acanthocarpa</i>	Arizona, Pima County, Headquarters, Organ Pipe Cactus National Monument, <b>neotype locality for <i>Opuntia echinocarpa</i> var. <i>major</i> as designated by L. Benson</b>	30	31.9545° -112.8005°	513	W. F. Steenbergh 5-2662-1 (RSA)

**Table 1.** Locations, sample sizes, and herbarium vouchers of populations sampled for the morphological analysis of *Cylindropuntia acanthocarpa*.

Site no.	Taxon	Locality	N	Latitude, longitude	Elev. (m)	Voucher(s) collector and number
11	<i>C. acanthocarpa</i>	Arizona, Pinal County, 3 km ESE of Florence Junction; ca. 40 km NE of Sacaton, <b>approximate type locality for <i>Opuntia acanthocarpa</i> var. <i>ramosa</i></b>	30	33.2488° -111.3043°	600	MAB 17654 (ASU)
12	<i>C. acanthocarpa</i>	Arizona, Pima County, 500m SSW of Gates Pass, 16 km WNW of downtown Tucson	30	32.2176° -111.1027°	910	MAB 8114 (ASU)
13	<i>C. acanthocarpa</i>	Arizona, Pinal County, 13 km NNE of Sacaton, Goldmine Mountain, 4 km north of Rock Peak	30	33.1720° -111.6404°	524	MAB 18667 (ASU)
14	<i>C. acanthocarpa</i>	Arizona, Pinal County, 1.9 km WNW of Summit of Little Tabletop, 60 km ESE of Gila Bend	30	32.7110° -112.1598°	694	MAB 18665 (ASU)
15	<i>C. acanthocarpa</i>	Arizona, Yavapai County, Black Canyon, 600 m NW of Bumble Bee, <b>epineotype locality for <i>Opuntia thornberi</i></b>	30	34.2063° -112.1567°	835	MAB 16147 (ASU, RSA)
16	<i>C. acanthocarpa</i>	Arizona, Yavapai County, along Bloody Basin Road, 850 m east of the Agua Fria River, 50 km SE of Prescott	30	34.2514° -112.0552°	1015	MAB 17657 (ASU)
17	<i>C. acanthocarpa</i>	Arizona, Gila County, 9.4 km NNE of Roosevelt between Dagger Wash and Salome Creek, 48 km NNW of Globe	30	33.7427° -111.0889°	800	MAB 17681 (ASU)
18	<i>C. acanthocarpa</i>	Arizona, Maricopa County, 7 km SSW of Horseshoe Dam, 50 km NNE of downtown Phoenix	30	33.9201° -111.7249°	915	MAB 17870 (ASU)
19	<i>C. acanthocarpa</i>	Arizona, Yavapai County, 50 km SW of Prescott, 16 km SSW of Hillside,	30	34.2761° -112.9053°	1001	MAB 18269.1 (ASU)
20	<i>C. echinocarpa</i>	California, San Bernardino County, 9 km WSW of South Pass, 32 km west of Needles, just south of Interstate 40, <b>neotype locality for <i>Opuntia echinocarpa</i></b>	30	34.8375° -114.9848°	670	MAB 13838 (ASU), L. Benson 10374 (RSA)
21	<i>C. echinocarpa</i>	Nevada, Clark County, just north of the town of Blue Diamond, 23 km SW of central Las Vegas	29	36.0517° -115.4082°	1035	MAB 13670 (ASU)
22	<i>C. echinocarpa</i>	California, San Diego County, Carrizo Valley, 1 km SE of Egg Mountain, 90 km east of central San Diego	30	32.8584° -116.2078°	210	MAB 7531 (ASU)

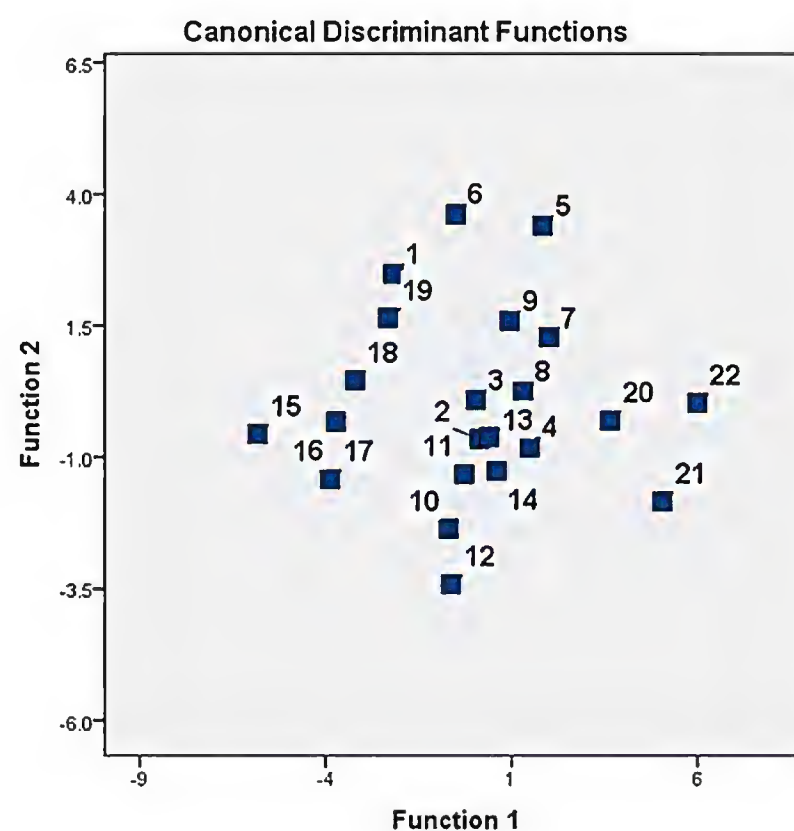
**Table 2.** Description of characters measured in the morphological analysis of *Cylindropuntia acanthocarpa*. Node is used here in reference to where branches originate from trunks or larger branches, not a stem node or areole. Except for individual height and width, characters were measured three times, each from separate areas on the trunk or from separate stems. Central spines were those centermost in the areole and were characterized by notably greater diameters of both the spines themselves and their sheaths, in comparison to those of the outermost or radial spines.

Character	Description
plant height	height of the individual from ground level to the tip of the tallest stem, excluding spines
plant width	width of the plant at its widest point, excluding spines
branch angle	angle between trunk and primary branch, divaricate branches equaling 90°
distance between trunk branches (cm)	mean length of three inter-branch spaces along the main trunk or, if unavailable, those along primary branches
branches per trunk node	mean number of branches at each of three trunk nodes or, if unavailable or not easily visible, those along primary branches. Trunk nodes with 0 branches were not included.
stem length (mm)	mean length of three ultimate mature stem segments
stem diameter (mm)	mean diameter at widest portion of three ultimate mature stem segments
tubercle length (mm)	mean length of top-most penultimate tubercle from three stem segments
tubercle width (mm)	mean width of top-most penultimate tubercle from three stem segments
tubercle height (mm)	mean height of top-most penultimate tubercle from three stem segments
central spine number	mean number of central spines per areole from tubercles as described above
radial spine number	mean number of radial spines per areole from tubercles as described above
central spine length (mm)	mean length of longest central spine per areole from tubercles as described above
radial spine length (mm)	mean length of longest radial spine per areole from tubercles as described above
central spine diameter (0.01 mm)	mean diameter of longest central spine per areole from tubercles as described above
central spine sheath diameter (0.01 mm)	mean diameter of the sheath of the longest central spine per areole from tubercles as described above



## RESULTS

**Discriminant Function Analysis.**—Discriminant Function Analysis was first used to assess the groupings of populations. Figure 2 is a scatterplot of population centroids for functions 1 and 2, which represent 68% of the total variation. Populations 1 through 3 are the most representative of what has been classified under typical *Cylindropuntia acanthocarpa*. The population centroid for the type locality at Cactus Pass (population 1) falls close to those of traditionally defined as *C. acanthocarpa* var. *thornberi* (populations 15-19), and the centroid for the neotype locality (population 2) west of Hillside falls close to those of *C. acanthocarpa* var. *ramosa* (populations 10-14). The population centroid for the type locality for *C. acanthocarpa* var. *coloradensis* (population 4) is close to those of *C. acanthocarpa* var. *acanthocarpa* and *C. acanthocarpa* var. *ramosa*. Populations 5 through 9 also fall within the geographical distribution of what has been traditionally classified under *Cylindropuntia acanthocarpa* var. *coloradensis*. Group centroids for population 4 and the neotype population of *C. echinocarpa* (population 20) are in close proximity, indicating that introgression may be influencing one or both populations. Populations 21 and 22 also represent *C. echinocarpa*. In general, results from the first DFA indicated that the most supportable PTG of populations appeared to align with the recognition of three subspecific taxa: *C. acanthocarpa* var. *acanthocarpa*, *C. acanthocarpa* var. *ramosa*, and *C. acanthocarpa* var. *thornberi* (Table 7).



**Figure 2.** Scatterplot of population centroids for DFA function 1 vs. function 2 defining groupings as populations. Functions 1 and 2 represent 68% of the total variation. Each symbol represents a population.

A discriminant function analysis was then run placing populations within groupings or potential taxa (PTGs). The PTGs were based on the grouping of population centroids from the first DFA and geographic distribution. Because of the lack of morphological correlation between populations of *C. acanthocarpa* var. *acanthocarpa* and those of traditional *C. acanthocarpa* var. *coloradensis*, individuals of the two taxa were combined. This DFA resulted in an overall correct classification of 88.2%, with correct classification for individuals of *C. acanthocarpa* var. *acanthocarpa* of 86.7% (Table 3). As expected, individuals of the outgroup *C. echinocarpa* were well-assembled, with only a single individual misclassified as *C. acanthocarpa* var. *acanthocarpa* and another as *C. acanthocarpa* var. *ramosa*. For individuals of the expanded *C. acanthocarpa* var. *acanthocarpa* group, 8.1% were misclassified as *C. acanthocarpa* var. *ramosa* and 4.4% were misclassified as *C. acanthocarpa* var. *thornberi*. The *C. acanthocarpa* var. *ramosa* group was the weakest, with 84.7% correctly classified individuals and all misclassified individuals being placed within the *C. acanthocarpa* var. *acanthocarpa* group. The *C. acanthocarpa* var. *thornberi* group had the highest percentage of correctly classified individuals (88.7%), with misclassified individuals being more evenly placed between the other two *C. acanthocarpa* groups. Figure 3 is a scatterplot of DFA function 1 vs. 2; the weighting of the characters is presented in Table 4. There was good separation among individuals of *C. acanthocarpa* var. *acanthocarpa*, *C. acanthocarpa* var. *thornberi*, and *C. echinocarpa* and rather poor separation between individuals of *C. acanthocarpa* var. *acanthocarpa* and *C. acanthocarpa* var. *ramosa*. However, when function 3 was added, resulting in a three-dimensional plot (Figure 4), separation of individuals between the two taxa became more apparent. Function 3 represented another 10% of the total variation.

A DFA with *Cylindropuntia acanthocarpa* var. *coloradensis* included as a group, along with the other currently accepted taxa based on Benson's (1982) taxonomy, resulted in an 83.6% overall correct classification among the four varieties of *C. acanthocarpa*. Individuals within the *C. acanthocarpa* var. *acanthocarpa* group were only 42.9% correctly classified (Table 5).

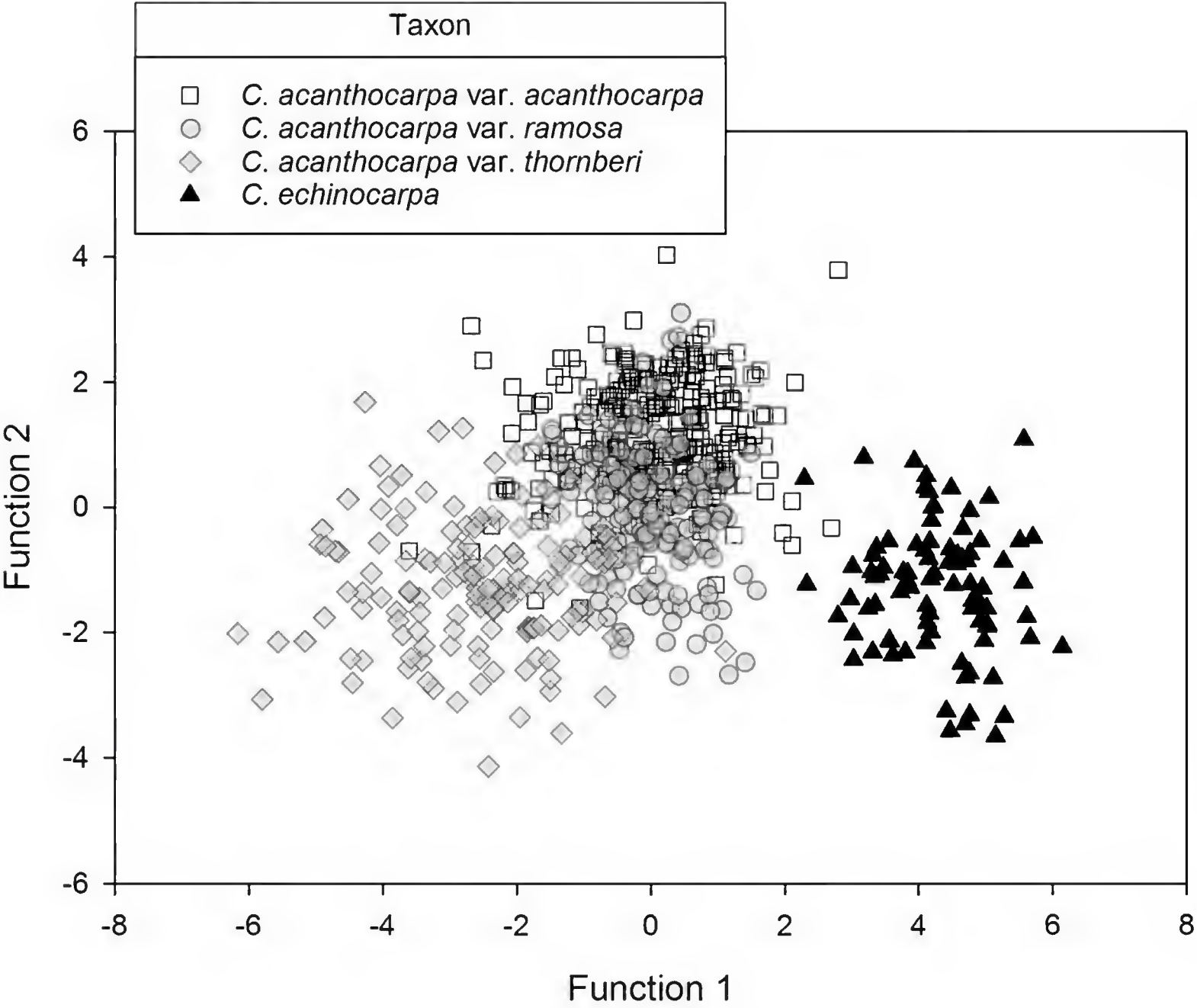
Because of the low correct classification for individuals of *Cylindropuntia acanthocarpa* var. *ramosa*, with all of the misclassified individuals classified as *C. acanthocarpa* var. *acanthocarpa*, a final DFA was run with individuals of *C. acanthocarpa* var. *ramosa* and *C. acanthocarpa* var. *coloradensis* pre-classified as *C. acanthocarpa* var. *acanthocarpa*. In this DFA, individuals of *C. acanthocarpa* var. *acanthocarpa* were 97.1% correctly classified and those of *C. acanthocarpa* var. *thornberi* were 86.0% correctly classified (Table 6).

Table 7 summarizes the definitions of taxa, by study population, for the DFA using populations as the grouping variable and the resulting DFA of taxa as defined by population centroids; for the DFA using taxa as circumscribed by recent taxonomic treatments, which follow Benson (1982); and for the DFA lumping both *C. acanthocarpa* var. *coloradensis* and *C. acanthocarpa* var. *ramosa* into *C. acanthocarpa* var. *acanthocarpa*.

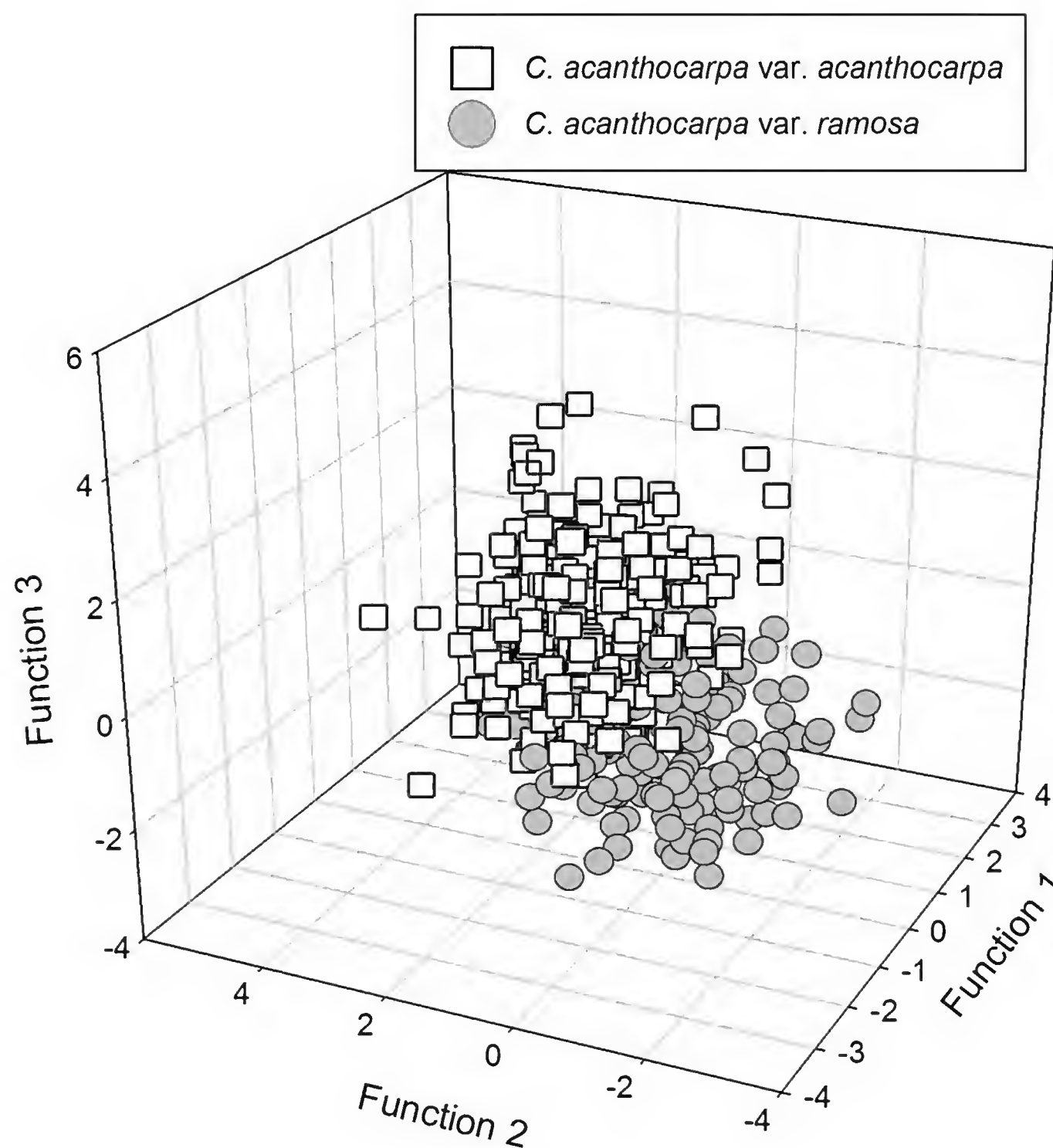
**Table 3.** Classification results of discriminant function analysis: predicted group membership by number of individuals correctly classified and by percentage of individuals correctly classified (bold); the dependent (grouping) variable defined as taxa with traditional populations of *C. acanthocarpa* var. *coloradensis* included within *C. acanthocarpa* var. *acanthocarpa*.

Taxon	Predicted group membership				Total
	var. <i>acanthocarpa</i>	var. <i>ramosa</i>	var. <i>thorneri</i>	<i>C. echinocarpa</i>	
By number of individuals					
var. <i>acanthocarpa</i>	235	22	12	2	271
var. <i>ramosa</i>	23	127	0	0	150
var. <i>thorneri</i>	9	7	133	1	150
<i>C. echinocarpa</i>	1	1	0	87	89
By percentage of individuals					
var. <i>acanthocarpa</i>	<b>86.7</b>	8.1	4.4	0.7	100.0
var. <i>ramosa</i>	15.3	<b>84.7</b>	0.0	0.0	100.0
var. <i>thorneri</i>	6.0	4.7	<b>88.7</b>	0.7	100.0
<i>C. echinocarpa</i>	1.1	1.1	0.0	<b>97.8</b>	100.0
88.2% overall correct classification					





**Fig. 3.** Scatterplot of functions 1 and 2 for DFA defining populations into four groupings (taxa), *Cylindropuntia acanthocarpa* var. *acanthocarpa*, *C. acanthocarpa* var. *ramosa*, *C. acanthocarpa* var. *thorneri*, and *C. echinocarpa*. Each symbol represents an individual.



**Figure 4.** Scatterplot of functions 1, 2, and 3 for DFA defining populations into four groupings (taxa), only individuals of *Cylindropuntia acanthocarpa* var. *acanthocarpa* and *C. acanthocarpa* var. *ramosa* shown. Each symbol represents an individual.

**Table 4.** Weighting of characters for DFA functions 1 and 2. Numbers represent standardized canonical discriminant function coefficients. Weighting is represented by the absolute value of the difference between the coefficients of F1 and F2. Those with the greatest weighting figure most prominently in the analyses.

Character	F1	F2	Absolute value of (F1-F2)
Tubercle length	-0.83	0.354	1.184
Central spine number	0.547	-0.049	0.596
Central spine sheath diameter	-0.097	0.329	0.426
Central spine diameter	0.019	-0.299	0.318
Tubercle width	0.069	0.366	0.297
Branch angle	-0.003	-0.24	0.237
Branches per trunk internode	0.227	0.003	0.224
Central spine length	0.33	0.119	0.211
Stem length	-0.139	-0.332	0.193
Stem diameter	0.245	0.406	0.161
Tubercle height	-0.014	0.144	0.158
Radial spine number	0.109	0.264	0.155
Radial spine length	-0.091	-0.217	0.126
Distance between trunk branches	-0.041	0.013	0.054



**Table 5.** Classification results of discriminant function analysis: predicted group membership by number of individuals correctly classified and by percentage of individuals correctly classified (bold); the dependent (grouping) variable defined as taxa according to Benson's (1982) taxonomy with the exception that his *C. acanthocarpa* var. *major* is under the name *C. acanthocarpa* var. *ramosa*.

Taxon	Predicted group membership					Total
	var. <i>acanthocarpa</i>	var. <i>coloradensis</i>	var. <i>ramosa</i>	var. <i>thornberi</i>	<i>C.</i> <i>echinocarpa</i>	
By number of individuals correctly classified						
var. <i>acanthocarpa</i>	39	21	19	12	0	91
var. <i>coloradensis</i>	9	161	9	0	1	180
var. <i>ramosa</i>	4	13	133	0	0	150
var. <i>thornberi</i>	11	1	6	132	0	150
<i>C. echinocarpa</i>	0	1	1	0	87	89
By percentage of individuals correctly classified						
var. <i>acanthocarpa</i>	<b>42.9</b>	23.1	20.9	13.2	0.0	100.0
var. <i>coloradensis</i>	5.0	<b>89.4</b>	5.0	0.0	0.6	100.0
var. <i>ramosa</i>	2.7	8.7	<b>88.7</b>	0.0	0.0	100.0
var. <i>thornberi</i>	7.3	0.7	4.0	<b>88.0</b>	0.0	100.0
<i>C. echinocarpa</i>	0.0	1.1	1.1	0.0	<b>97.8</b>	100.0
83.6% overall correct classification						

**Table 6.** Classification results of discriminant function analysis: predicted group membership by number of individuals correctly classified and by percentage of individuals correctly classified (bold); the dependent (grouping) variable defined as taxa with populations of *C. acanthocarpa* var. *coloradensis* and *C. acanthocarpa* var. *ramosa* included within *C. acanthocarpa* var. *acanthocarpa*.

Taxon	Predicted group membership			Total
	var. <i>acanthocarpa</i>	var. <i>thornberi</i>	<i>C. echinocarpa</i>	
By number of individuals				
var. <i>acanthocarpa</i>	409	10	2	421
var. <i>thornberi</i>	21	129	0	150
<i>C. echinocarpa</i>	2	0	87	89
By percentage of individuals				
var. <i>acanthocarpa</i>	<b>97.1</b>	2.4	0.5	100.0
var. <i>thornberi</i>	14.0	<b>86.0</b>	0.0	100.0
<i>C. echinocarpa</i>	2.2	0.0	<b>97.8</b>	100.0
94.7% correct classification				

**Multiple Analysis of Variance.**—Duncan’s multiple range test showed that 12 of the 14 stem characters were significantly different at  $P < 0.001$  for one or more of the four taxa. Selected homogeneous subsets for stem characters are presented in Table 8. As expected, the outgroup *Cylindropuntia echinocarpa* possessed the greatest number of significantly different mean values, with 10 of the 14 characters being significantly different from any of the *C. acanthocarpa* taxa.

The most significant differences among the infraspecific taxa in *C. acanthocarpa* were associated with tubercle morphology and spine number. The branch angles were narrowest in *C. acanthocarpa* var. *acanthocarpa*, including populations originally classified as *C. acanthocarpa* var. *coloradensis*, and widest in *C. acanthocarpa* var. *ramosa*. Stem diameter was also diagnostic among the three infraspecific taxa, with *C. acanthocarpa* var. *acanthocarpa* having the thickest stems and *C. acanthocarpa* var. *ramosa* the thinnest. Individuals of *C. acanthocarpa* var. *acanthocarpa* had the longest central spines, while central spine and spine sheath diameters were smallest in *C. acanthocarpa* var. *ramosa*. Spine length data from our samples supports that the type description of *O. echinocarpa* var. *major* belongs within *C. acanthocarpa* var. *acanthocarpa*.

## DISCUSSION AND CONCLUSIONS

Our analysis did not provide sufficient evidence for a morphological distinction between *Cylindropuntia acanthocarpa* var. *acanthocarpa* and *C. acanthocarpa* var. *coloradensis*; we therefore combined them under *C. acanthocarpa* var. *acanthocarpa*. The data provide the strongest support for preserving *C. acanthocarpa* var. *thornberi* and reasonable support for the preservation of *C. acanthocarpa* var. *ramosa*, populations of which have been under the name *C. acanthocarpa* var. *major* in recent treatments. There is an 85% correct classification for sampled individuals of *C. acanthocarpa* var. *ramosa*, and there are five characters that possess mean values that are significantly different from all other taxa.

The taxonomy of this group is complicated by the location of the type populations, with both the original and neotype populations for *Opuntia acanthocarpa* occurring at the edge of the geographic range for the typical variety, near where these individuals intergrade morphologically with *Cylindropuntia acanthocarpa* var. *thornberi*. The choice of type locality for *O. acanthocarpa* var. *coloradensis* was also unfortunate because it was also the neotype locality for *Opuntia echinocarpa*, and putative hybrids (*C. ×deserta* [Griffiths] F. M. Knuth), as indicated by intermediate morphology, have been documented in the areas of sympatry between *C. acanthocarpa* and *C. echinocarpa* (Baker 2016, Baker et al. 2012, Pinkava 1999, Pinkava & Baker 2012).

Although there is some confusion with respect to morphology and taxonomy for the original type and neotype localities of *Opuntia acanthocarpa*, Engelmann’s original description of *Opuntia acanthocarpa* fits best with our group of populations we define as *Cylindropuntia acanthocarpa* var. *acanthocarpa*. Engelmann used the French metric system (Trelease and Gray 1887), for which at the time a “line” was ca. 2.3 mm (Hallock and Wade 1906). Using this conversion, Engelmann’s description of stem diameter for *O. acanthocarpa* was 25.4 mm, and the central spine length was

between 25.4 and 31.8 mm, which most closely match the mean values for those of *C. acanthocarpa* var. *acanthocarpa* as defined in our analyses. The tubercle length (20.7- 23 mm) in the original description is far too short for *C. acanthocarpa* var. *thornberi*, which is the other variety that occurs in or near the areas of both the original type and the neotype localities.

It may be prudent to maintain only two infraspecific taxa within *Cylindropuntia acanthocarpa*, but we have chosen to be conservative in the redefinition of taxa. It is of interest that our current taxonomic position reflects that of Benson’s original edition of the Cacti of Arizona (1940), although he placed chollas (*Cylindropuntia*) within *Opuntia* and gave species rank to *O. ramosa* Peebles.

**Table 7.** Definition of *Cylindropuntia* taxa, by study population, as circumscribed by recent taxonomic treatments, which follow Benson (1982); and by our assessment of the literature and DFA analyses.

Site no.	Taxa as defined by DFA analyses of populations and for the subsequent grouping of centroids	Taxa as defined by Benson (1982)	Taxa as defined by DFA analysis that lumped both <i>C. acanthocarpa</i> var. <i>coloradensis</i> and <i>C. acanthocarpa</i> var. <i>ramosa</i> into <i>C. acanthocarpa</i> var. <i>acanthocarpa</i>
1	<i>C. acanthocarpa</i> var. <i>acanthocarpa</i>	<i>C. acanthocarpa</i> var. <i>acanthocarpa</i>	<i>C. acanthocarpa</i> var. <i>acanthocarpa</i>
2	<i>C. acanthocarpa</i> var. <i>acanthocarpa</i>	<i>C. acanthocarpa</i> var. <i>acanthocarpa</i>	<i>C. acanthocarpa</i> var. <i>acanthocarpa</i>
3	<i>C. acanthocarpa</i> var. <i>acanthocarpa</i>	<i>C. acanthocarpa</i> var. <i>acanthocarpa</i>	<i>C. acanthocarpa</i> var. <i>acanthocarpa</i>
4	<i>C. acanthocarpa</i> var. <i>acanthocarpa</i>	<i>C. acanthocarpa</i> var. <i>coloradensis</i>	<i>C. acanthocarpa</i> var. <i>acanthocarpa</i>
5	<i>C. acanthocarpa</i> var. <i>acanthocarpa</i>	<i>C. acanthocarpa</i> var. <i>coloradensis</i>	<i>C. acanthocarpa</i> var. <i>acanthocarpa</i>
6	<i>C. acanthocarpa</i> var. <i>acanthocarpa</i>	<i>C. acanthocarpa</i> var. <i>coloradensis</i>	<i>C. acanthocarpa</i> var. <i>acanthocarpa</i>
7	<i>C. acanthocarpa</i> var. <i>acanthocarpa</i>	<i>C. acanthocarpa</i> var. <i>coloradensis</i>	<i>C. acanthocarpa</i> var. <i>acanthocarpa</i>
8	<i>C. acanthocarpa</i> var. <i>acanthocarpa</i>	<i>C. acanthocarpa</i> var. <i>coloradensis</i>	<i>C. acanthocarpa</i> var. <i>acanthocarpa</i>
9	<i>C. acanthocarpa</i> var. <i>acanthocarpa</i>	<i>C. acanthocarpa</i> var. <i>coloradensis</i>	<i>C. acanthocarpa</i> var. <i>acanthocarpa</i>
10	<i>C. acanthocarpa</i> var. <i>ramosa</i>	<i>C. acanthocarpa</i> var. <i>major</i>	<i>C. acanthocarpa</i> var. <i>acanthocarpa</i>



**Table 7.** Definition of *Cylindropuntia* taxa, by study population, as circumscribed by recent taxonomic treatments, which follow Benson (1982); and by our assessment of the literature and DFA analyses.

Site no.	Taxa as defined by DFA analyses of populations and for the subsequent grouping of centroids	Taxa as defined by Benson (1982)	Taxa as defined by DFA analysis that lumped both <i>C. acanthocarpa</i> var. <i>coloradensis</i> and <i>C. acanthocarpa</i> var. <i>ramosa</i> into <i>C. acanthocarpa</i> var. <i>acanthocarpa</i>
11	<i>C. acanthocarpa</i> var. <i>ramosa</i>	<i>C. acanthocarpa</i> var. <i>major</i>	<i>C. acanthocarpa</i> var. <i>acanthocarpa</i>
12	<i>C. acanthocarpa</i> var. <i>ramosa</i>	<i>C. acanthocarpa</i> var. <i>major</i>	<i>C. acanthocarpa</i> var. <i>acanthocarpa</i>
13	<i>C. acanthocarpa</i> var. <i>ramosa</i>	<i>C. acanthocarpa</i> var. <i>major</i>	<i>C. acanthocarpa</i> var. <i>acanthocarpa</i>
14	<i>C. acanthocarpa</i> var. <i>ramosa</i>	<i>C. acanthocarpa</i> var. <i>major</i>	<i>C. acanthocarpa</i> var. <i>acanthocarpa</i>
15	<i>C. acanthocarpa</i> var. <i>thornberi</i>	<i>C. acanthocarpa</i> var. <i>thornberi</i>	<i>C. acanthocarpa</i> var. <i>thornberi</i>
16	<i>C. acanthocarpa</i> var. <i>thornberi</i>	<i>C. acanthocarpa</i> var. <i>thornberi</i>	<i>C. acanthocarpa</i> var. <i>thornberi</i>
17	<i>C. acanthocarpa</i> var. <i>thornberi</i>	<i>C. acanthocarpa</i> var. <i>thornberi</i>	<i>C. acanthocarpa</i> var. <i>thornberi</i>
18	<i>C. acanthocarpa</i> var. <i>thornberi</i>	<i>C. acanthocarpa</i> var. <i>thornberi</i>	<i>C. acanthocarpa</i> var. <i>thornberi</i>
19	<i>C. acanthocarpa</i> var. <i>thornberi</i>	<i>C. acanthocarpa</i> var. <i>thornberi a</i>	<i>C. acanthocarpa</i> var. <i>thornberi</i>
20	<i>C. echinocarpa</i>	<i>C. echinocarpa</i>	<i>C. echinocarpa</i>
21	<i>C. echinocarpa</i>	<i>C. echinocarpa</i>	<i>C. echinocarpa</i>
22	<i>C. echinocarpa</i>	<i>C. echinocarpa</i>	<i>C. echinocarpa</i>

**Table 8.** Character means by *Cylindropuntia* taxon. Means in bold are significantly different ( $p < 0.001$ ) from means of all other taxa. Standard deviations are given in parentheses.

Character	Taxon			
	<i>C. acanthocarpa</i> var. <i>acanthocarpa</i>	<i>C. acanthocarpa</i> var. <i>ramosa</i>	<i>C. acanthocarpa</i> var. <i>thorneri</i>	<i>C. echinocarpa</i>
Plant height (cm)	116.5 (33.5)	121.7 (34.0)	83.0 (33.3)	82.2 (29.2)
Plant width (cm)	151.1 (54.2)	168.6 (53.4)	132.2 (53.1)	86.5 (36.9)
Branch angle (°)	<b>36.2</b> (9.2)	44.1 (11.8)	44.5 (12.7)	<b>60.5</b> (15.0)
Distance between trunk branches (cm)	16.6 (5.7)	16.9 (6.1)	15.4 (5.3)	<b>9.4</b> (2.9)
Branches per trunk node	1.7 (.53)	1.6 (.51)	1.5 (.46)	<b>2.6</b> (.83)
Stem length (mm)	105.2 (25.4)	102.3 (28.4)	<b>125.6</b> (33.6)	<b>57.5</b> (14.0)
Stem diameter (mm)	<b>24.7</b> (3.9)	<b>19.6</b> (2.5)	<b>21.3</b> (3.2)	<b>23.4</b> (3.0)
Tubercle length (mm)	<b>27.5</b> (5.2)	<b>22.8</b> (3.0)	<b>35.6</b> (6.5)	<b>12.1</b> (2.6)
Tubercle width (mm)	<b>6.6</b> (1.3)	<b>4.9</b> (0.8)	6.0 (1.4)	6.1 (0.9)
Tubercle height (mm)	6.7 (1.2)	<b>5.3</b> (0.8)	6.4 (1.3)	<b>5.8</b> (1.2)
Central spine number	<b>7.0</b> (1.8)	<b>5.4</b> (1.3)	<b>3.5</b> (1.5)	<b>7.8</b> (1.8)
Radial spine number	<b>9.0</b> (1.7)	7.5 (1.4)	<b>5.7</b> (1.5)	7.9 (1.8)
Central spine length (mm)	25.7 (5.8)	19.3 (5.7)	19.1 (7.2)	24.6 (7.3)
Radial spine length (mm)	16.9 (3.7)	17.1 (3.9)	<b>14.5</b> (3.3)	<b>12.6</b> (3.1)
Central spine diameter (mm)	0.62 (0.129)	0.48 (0.106)	0.64 (0.160)	0.52 (0.152)
Central spine sheath diameter (mm)	<b>1.02</b> (0.196)	<b>0.72</b> (0.191)	<b>0.94</b> (0.238)	<b>0.84</b> (0.166)

## NOMENCLATURAL SUMMARY

Types are cited using the numbering system of each herbarium, and in brackets the JSTOR Global Plants Initiative numbering system of images online is given (Global Plants Initiative 2017).

1. *Cylindropuntia acanthocarpa* (Engelmann & J. M. Bigelow) F. M. Knuth, Kaktus-ABC [Backeberg & F. M. Knuth] 124. 1936.

*Opuntia acanthocarpa* Engelmann & J. M. Bigelow, Proc. Amer. Acad. Arts 3: 308. 1856. TYPE. Arizona, Mohave County, "mountains of Cactus Pass," January 1854, *J. M. Bigelow s. n.* (all original material lost). NEOTYPE designated by Benson, (1982). Arizona, Yavapai County, 9.5 miles west of Hillside, *L. Benson 10874*, (NEOTYPE: POM274024! [=RSA-0008890]; ISONEOTYPES: CAS500838! [=CAS-0006948], ARIZ 74828! [=ARIZ-BOT-0005737]).

The original material of *Opuntia acanthocarpa* was collected in January 1854 by J. M. Bigelow near Cactus Pass, Mohave County, Arizona, during the Whipple expedition to survey for a railroad route from the Mississippi River to the Pacific Ocean (Engelmann 1856a, 1856b; Engelmann & Bigelow 1856). To date, the original material has not been found. The name was first published in Engelmann's Synopsis of the Cactaceae of the territory of the United States (Engelmann 1856a), which was reprinted, apparently in the same year, by Metcalf and Company (Engelmann 1856b). Although within the Synopsis, Engelmann ascribes the name *Opuntia acanthocarpa* to the report on the botany of the Whipple expedition (Engelmann & Bigelow 1856), the report was not published prior to the Synopsis. This is evident in Engelmann's own words in the Synopsis, page 260:

"Most of the materials brought together by these different explorers have come into the hands of the writer; but few of the discoveries made since 1847 and 1848 have been given to the public;—partly because the material on hand very often was incomplete, and partly because it seemed desirable to publish the whole in an elaborate form with the Reports of the Boundary Commission and those of the Pacific Railroad Surveys. These reports are now in preparation; but the splendid plates which are to illustrate the natural history of these plants cannot be finished for some time; it is therefore deemed advisable now to publish short descriptions of the new species, and systematically to arrange them with those before known."

The significance of the chronological order of these publications is in the designation of the type. As mentioned above, there are no original specimens, and the "splendid plates" that were referred to by Engelmann were not finished and not included in the Synopsis and therefore cannot serve as types. Thus the lectotypifications of *Opuntia acanthocarpa* and *O. echinocarpa* Engelmann & J. M. Bigelow by Crook and Mottram (1995, 1996) with illustrations from Engelmann and Bigelow (1856) have no standing (Holmgren et al. 2012).



**1A. *Cylindropuntia acanthocarpa* var. *acanthocarpa*.** Autonym based on same type as the species (Figures 5A; 6A, B, C).

***Opuntia echinocarpa* var. *major*** Engelman, Proc. Amer. Acad. Arts 3: 305 1856. TYPE. Arizona, California or Sonora, Mexico, "In the valley of the Lower Colorado" river, *Schott s. n.* (no original material has been found). Engelman (1859) elaborated on the type as "In the deserts on both sides of the Colorado, and in Sonora, *Schott*."

Because all original material is missing and because we believe that a previously designated neotype was done erroneously, we designate a new neotype here.

United States, California, Imperial County, Picacho State Recreation Area, south of Colorado River, Taylor Lake Overlook, 16 April 2005, *Larry Hendrickson et al.* 3223, (NEOTYPE designated here: NEOTYPE: ASU0089312! [=ASU-293568]; ISONEOTYPE: SD191490). We have chosen this specimen because it has both flowers and branching stems and comes from the approximate type locality as specified by Engelman.

We reject Benson's choice of a neotype (Benson 1969, pg. 20): Arizona. Pima County, near border of northwestern Sonora [Mexico], "W. F. Steenbergh 5-2552-1, 26 May 1962, Headquarters of the Organ Pipe Cactus National Monument, Arizona (POM306088! [=RSA-008882]). The spine length data from our samples indicate that the type description of *O. echinocarpa* var. *major* belongs within *C. acanthocarpa* var. *acanthocarpa*. Benson's neotype falls within the morphological description of *C. acanthocarpa* var. *ramosa*. In addition, Schott collected the material, from which Engelman originally described that taxon, from the area around the Colorado River, where only *C. acanthocarpa* var. *acanthocarpa* occurs.

***Opuntia echinocarpa* var. *robustior*** J. M. Coulter, Contr. U. S. Natl. Herb. 3(7): 446. 1896. A superfluous new name proposed by Coulter for *Opuntia echinocarpa* var. *major* Engelman. The rules of nomenclature as we now use them were not in effect at that time. Coulter seems to have believed that because the epithet "*major*" had been used for a variety of *O. phaeacantha* it could not be used again in another species in the genus. Coulter does list specimens he examined, only the first of which represents *Cylindropuntia acanthocarpa*: Arizona (G. R. Vasey of 1881, Yuma) (US3046040!), annotated by J. M. Coulter as *Opuntia echinocarpa* [var.] *major*). The other specimens listed by Coulter represent *Cylindropuntia echinocarpa*: Newberry, 1858 [Mojave Valley, Camp 60, 23 March 1858] (MO-5254054!); Lemmon, 1878 [California desert] (MO-5254055!); with no collector given, 1880 [White Water Desert to San Geronio Pass, California, 10 Nov 1880], almost certainly collected by Charles Parry, who was at the locality on the same date. (MO5254053!); Parish Bros., 1882 [S. B. & W. F. Parish, San Bernardino, Vallecito] (MO5234057!)

***Opuntia acanthocarpa* var. *coloradensis*** L. D. Benson, Cacti Ariz. ed. 3. 20. 1969. TYPE. California, 23 miles west of Needles, 14 July 1940, *L. Benson 10375* (HOLOTYPE: POM244022! [=RSA0008891]; ISOTYPE: ARIZ137142!) (Figure 6).

***Opuntia acanthocarpa* var. *major*** (Engelmann & J. M. Bigelow) L. D. Benson, Cacti Ariz. ed. 3. 20. 1969.

***Cylindropuntia acanthocarpa* var. *coloradensis*** (L. D. Benson) Pinkava, Ariz.-Nev. Acad. Sci. 32(1):42. 1999.

***Cylindropuntia acanthocarpa* var. *major*** (Engelmann) Pinkava, Ariz.-Nev. Acad. Sci. 32(1): 42. 1999.

***Cylindropuntia acanthocarpa* subsp. *major*** (Engelmann & J. M. Bigelow) U. Guzmán, Cactaceae Syst. Init. 16: 16. 2003.

***Cylindropuntia acanthocarpa* subsp. *coloradensis*** (L. D. Benson) U. Guzmán, Cactaceae Syst. Init. 16: 16. 2003.

**1B. *Cylindropuntia acanthocarpa* var. *ramosa*** (Peebles) Backeberg, Cactaceae (Backeberg) 1: 181. 1958 (Figures 5B, 6D).

***Opuntia acanthocarpa*** Engelmann & J. M. Bigelow **var. *ramosa*** Peebles, Cact. Succ. J. (Los Angeles) 9: 37. 1937. TYPE. Arizona, Pinal County, near Sacaton, cultivated, 1920, *A. R. Leding SF 2*. (TYPE SHEET: US 1699996! [=US-00115774]) The type sheet has specimens collected on more than one date and thus represents multiple gatherings: Mounted stem with single dry flower, is here designated as LECTOTYPE; ISOLECTOTYPE: stems with flowers (ARIZ 94443! [=ARIZ-Bot-0005731]). The lectotype material apparently collected in 1920 and the additional material (fruits, flowers and seeds) collected 22 March 1927, June 1934, and 30 April 1937 has been added in three separate packets.

**1C. *Cylindropuntia acanthocarpa* var. *thornberi*** (Thornber & Bonker) Backeberg, Cactaceae (Backeberg) 1: 184. 1958 (Figures 5C, 6E).

***Opuntia thornberi*** Thornber & Bonker, Fantastic Clan: 133, 148. 1932. TYPE. upper illustration on page 135 of Thornber & Bonker (1932) [Note that Thornber & Bonker (1932) stated that the name had recently been published but no such publication has been found]; no type locality given, but Thornber & Bonker (1932) described populations as occurring on arid, sandy, or gravelly and rocky soils along the foothills and broad desert mesas in south central Arizona. EPITYPE designated by Crook & Mottram (1995): “Arizona, Yavapai County, Bumblebee, 2700 ft, June 16, 1939”, *Lyman Benson 9671*, POM 274081! [=RSA-0008883, labelled “neotype”]; ISOEPITYPE: ARIZ 158257!).

***Opuntia acanthocarpa* var. *thornberi*** (Thornber & Bonker) L. D. Benson, Proc. Calif. Acad. Sci. ser. 4, 25: 247. 1944.

***Cylindropuntia acanthocarpa* subsp. *thornberi*** (Thornber & Bonker) Lodé, Cact.-Avent. Int. 98 (Suppl.): 3. 2013.

2. *Cylindropuntia echinocarpa* (Engelmann & J. M. Bigelow) F. M. Knuth, Kaktus-ABC [Backeberg & F. M. Knuth] 124. 1936 (Figures 5D, 6F).

*Opuntia echinocarpa* Engelmann & J. M. Bigelow, Syn. Cact. U. S. 49. 1856. TYPE. Apparently Arizona, near mouth of Bill Williams River at Colorado River, Bigelow *s.n.* (original material not found). NEOTYPE designated by Benson (1982). California, San Bernardino County, 23 miles west of Needles, 1200 feet elevation, (in fruit) Lyman Benson 10374 (NEOTYPE: POM274071! [=RSA-008845]).

*Opuntia wigginsii* L. D. Benson, Cacti Ariz. ed. 3, 19, 32. 1969. TYPE. Arizona, Yuma County [probably now La Paz County], south of Quartzite, 900 feet elevation, Lyman & Evelyn L. Benson 16465, March 30, 1965 (HOLOTYPE: POM-296264! [=RSA-008930]) [a sheet composed of mature stems typical for *C. echinocarpa*, with some immature new growth]

*Cylindropuntia wigginsii* (L. D. Benson) H. Robinson, Phytologia 26:175. 1973.

EXCLUDED NAMES (accepted synonyms are preceded by “=”):

1. *Opuntia acanthocarpa* subsp. *ganderi* C. B. Wolf, Occas. Pap. Rancho Santa Ana Bot. Gard. 1(2): 75. 1938. TYPE. California, San Diego County, 3 mi. below the old Vallecito Stage Station, June 12, 1938, C. B. Wolf 9424, (HOLOTYPE: RSA- 18631! [=RSA-008893]).

*Opuntia acanthocarpa* var. *ganderi* (C. B. Wolf) L. D. Benson, Cact. Succ. J. (Los Angeles) 41: 33. 1969.

= *Cylindropuntia ganderi* (C. B. Wolf) Rebman & Pinkava var. *ganderi* J. Arizona-Nevada Acad. Sci. 33: 150. 2001.

2. *Opuntia echinocarpa* var. *parkeri* J. M. Coulter, Contr. U.S. Natl. Herb. 3(7): 446. 1896. TYPE. California, San Diego County, "east side of mountains facing desert," Sept 1879, C.F. Parker *s. n.* (HOLOTYPE: two sheets, apparently from the same gathering, MO-39397! [=MO-178063] with young fruits; and MO-39396! [=MO-178062] with stems.

= *Cylindropuntia californica* (Torrey & A. Gray) F. M. Knuth var. *parkeri* (J. M. Coulter) Pinkava, J. Arizona-Nevada Acad. Sci. 33: 150. 2001.

3. *Opuntia echinocarpa* var. *nuda* J. M. Coulter, Contr. U.S. Natl. Herb. 3(7): 446. 1896. Holotype. "in Herb. Brandegee, Lower California, near San Gregorio ([T. S.] Brandegee of 1889)". (Holotype: UC 110317!)

= *Cylindropuntia alcahes* var. *alcahes* (F. A. C. Weber) F. M. Knuth, Kaktus-ABC [Backeb. & Knuth] 127. 1936.

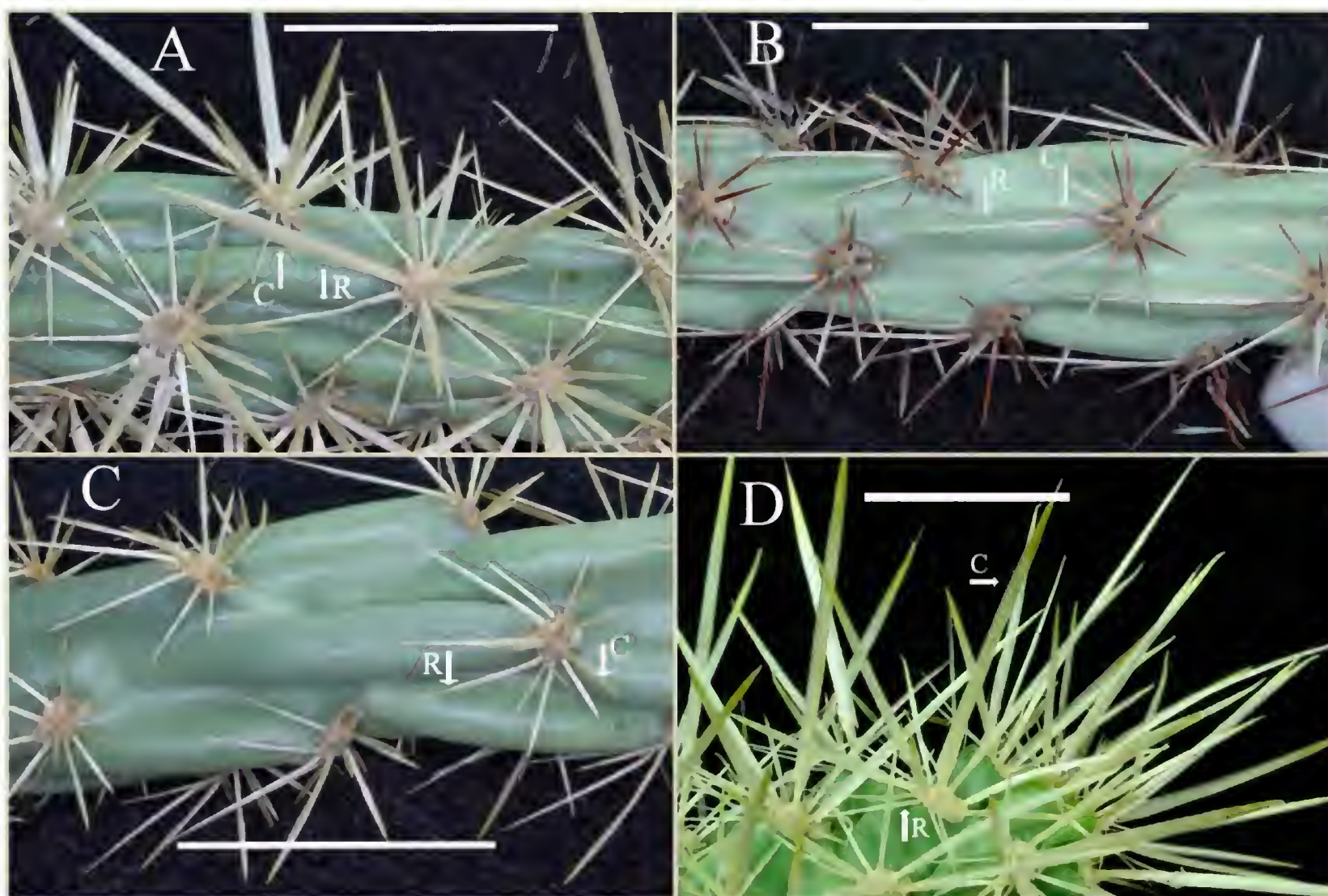
4. *Opuntia echinocarpa* var. *wolfii* L. D. Benson. Cact. Succ. J. (Los Angeles) 41: 33. 1969. Nom. Inval.



## KEY TO THE TAXA

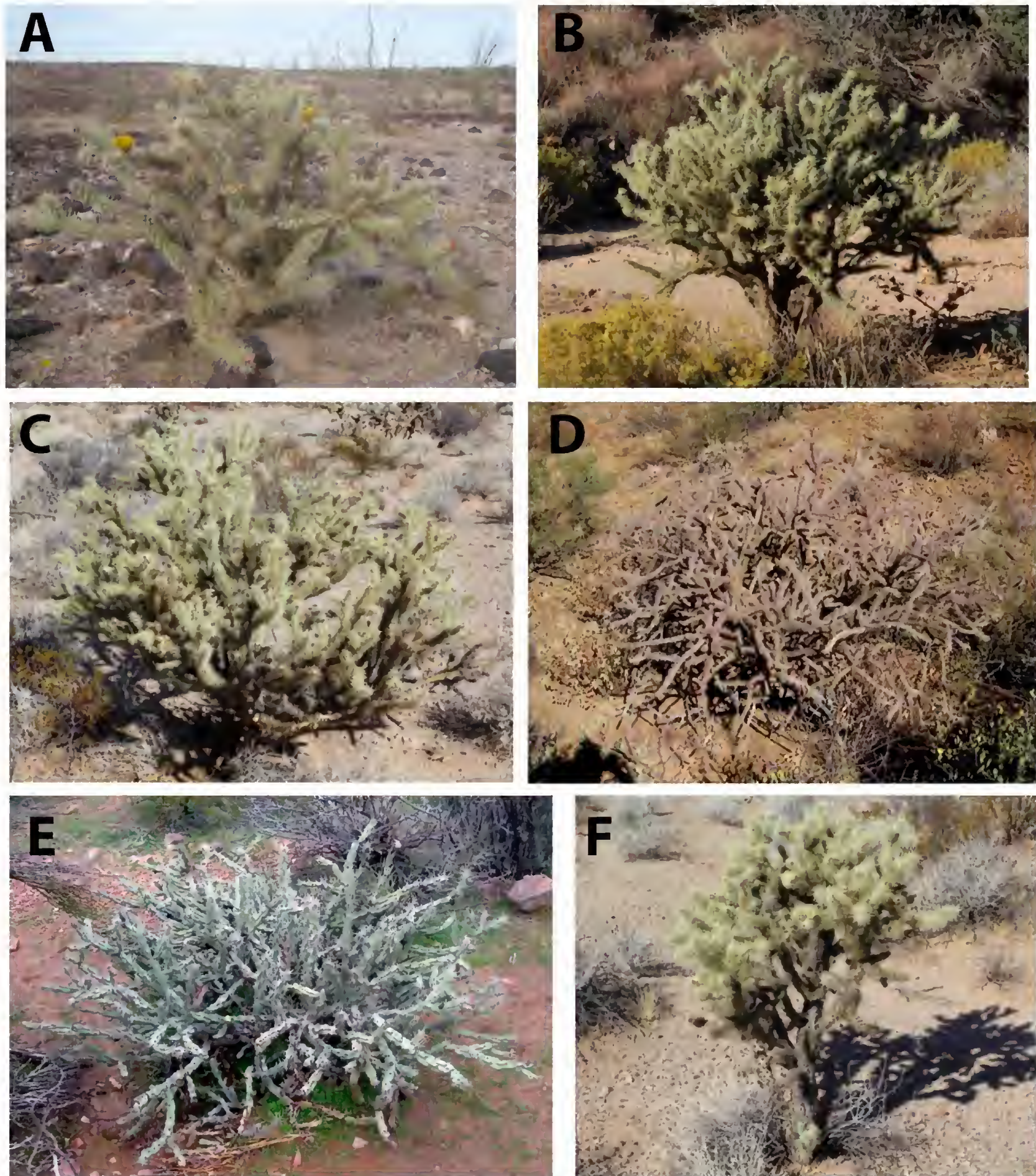
Because of overlapping character states, we recommend examining a number of individuals within a population in order to obtain an approximate average for key characters.

1. Branches generally two or more per trunk node, with trunk branch internodes mostly less than 10 cm in length; stem tubercles mostly less than 12 mm long; central spines averaging greater than seven in number. Primarily Mojave Desert but occurring sporadically southward into the Sonoran Desert to Baja California and Sonora, Mexico. ....*C. echinocarpa* (Figures 5D, 6F)
- 1' Branches generally one to two per trunk node, with trunk branch internodes mostly greater than 15 cm in length; stem tubercles mostly greater than 23 mm long; central spines averaging fewer than seven in number
2. Plants mostly less than 1 m tall and generally 50% or broader than tall; stem tubercles averaging 36 mm long; longest radial spines averaging 15 mm long. Endemic to the central highlands of Arizona.....*C. acanthocarpa* var. *thornberi* (Figures 5C, 6E)
- 2' Plants mostly more than 1 m tall and generally less than 50% broader than tall; stem tubercles averaging 27.5 mm or less in length; longest radial spines averaging greater than 17 mm in length
3. Branches mostly spreading less than 40° from the trunk; stem diameter mostly more than 20 mm; tubercles averaging 27.5 mm in length and 6.6 mm in width; spines generally more than 15 in number; central spine sheaths about 1 mm in diameter. Western Mojave Desert and eastern Sonoran Deserts of California, Nevada, Arizona, and northernmost Sonora. .... *C. acanthocarpa* var. *acanthocarpa* (Figures 5A; 6A, B, C)
- 3' Branches mostly spreading more than 40° from the trunk; stem diameter mostly less than 20 mm; tubercles averaging 22.8 mm in length and 4.9 mm in width; spines generally fewer than 13 in number; central spine sheaths about 0.7 mm in diameter. Western Sonoran Desert of Arizona and northernmost Sonora. ..*C. acanthocarpa* var. *ramosa* (Figures 5B, 6D)



**Figure 5.** Representative ultimate stem segments of *Cyllindropuntia acanthocarpa* and *C. echinocarpa*. A. *C. acanthocarpa* var. *acanthocarpa*. B. *C. acanthocarpa* var. *ramosa*; C. *C. acanthocarpa* var. *thornberi*. D. *C. echinocarpa*. Arrow with “C” = central spine, arrow with “R” = radial spine. Bars = 3 cm.





**Figure 6.** A. *Cylindropuntia acanthocarpa* var. *acanthocarpa* from Imperial County, California; B. *C. acanthocarpa* var. *acanthocarpa* from Mojave County, Arizona, near the original type locality (Cactus Pass); C. *C. acanthocarpa* var. *acanthocarpa* from San Bernardino County, California, at the type locality for *C. acanthocarpa* var. *coloradensis*; D. *C. acanthocarpa* var. *ramosa* from Pima County, Arizona; E. *C. acanthocarpa* var. *thornberi* from Gila County, Arizona; F. *C. echinocarpa* from San Bernardino County, California, neotype locality for the species.



## ACKNOWLEDGEMENTS

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This paper is dedicated to Dr. Donald J. Pinkava, who passed away 25 July 2017. He was beloved by all of his students and colleagues and provided an unfaltering example of hard work, dedication, and an insatiable curiosity about all things, especially those concerning the evolution and taxonomy of the Cactaceae. Known affectionately as “the Nipper,” he habitually insisted of students and colleagues, “Show me the data”.

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## INDEX TO FAMILIES OF THE VASCULAR PLANTS OF ARIZONA

Published treatments (**in bold**) can be found in volumes 26, 27, 29, 30, 32, 33, and 35 of the *Journal of the Arizona-Nevada Academy of Science* (JANAS) or in subsequent volumes (1–14) of CANOTIA. Unbolded entries indicate families with no treatments published to date. Figure numbers refer to illustrations in the “Key to Families of Vascular Plants in Arizona” in JANAS 35(2). All Vascular Plants of Arizona treatments are available as pdf files online ([http://www.canotia.org/vpa\\_project.html](http://www.canotia.org/vpa_project.html)).

- Acanthaceae CANOTIA 12:22-54. 2016. (T. Daniel)  
Aceraceae JANAS 29(1):2. 1995. (L.R. Landrum)  
Adiantaceae (Fig. 1)  
Agavaceae **Part 1: *Agave*** JANAS 32(1):1. 1999. (W. Hodgson)  
Aizoaceae  
Alismataceae CANOTIA 14:10. 2018 (J.Ricketson)  
Amaranthaceae (Fig. 4)  
Anacardiaceae CANOTIA 3(2):13. 2007. (J.L. Anderson)  
Apiaceae (Fig. 5)  
Apocynaceae JANAS 27(2):164. 1994. (S.P. McLaughlin)  
Araceae  
Araliaceae  
Arecaceae JANAS 32(1):22. 1999. (C.T. Mason, Jr.)  
Aristolochiaceae JANAS 32(1):24. 1999. (C.T. Mason, Jr.)  
Asclepiadaceae JANAS 27(2):169. 1994. (E. Sundell)  
Aspleniaceae  
Asteraceae (Figs. 6–7)  
Azollaceae CANOTIA 4(2):31. 2008. (G. Yatskievych and M.D. Windham)  
Berberidaceae JANAS 26(1):2. 1992. (J.E. LaFerriere; Fig. 9)  
Betulaceae JANAS 33(1):1. 2001. (J.W. Brasher)  
Bignoniaceae JANAS 32(1):26. 1999. (C.T. Mason, Jr.)  
Bixaceae JANAS 27(2):188. 1994. (W. Hodgson)  
Blechnaceae CANOTIA 4(2):35. 2008. (G. Yatskievych and M.D. Windham; Fig. 1)  
Boraginaceae (Fig. 9)  
Brassicaceae  
Bromeliaceae CANOTIA 3(2):23. 2007. (R. Gutierrez, Jr.)  
Buddlejaceae JANAS 26(1):5. 1992. (E.M. Norman)  
Burseraceae JANAS 32(1):29. 1999. (A. Salywon)  
Cactaceae **Part One: The Cereoid Cacti** JANAS 29(1):6. 1995. (D.J. Pinkava)  
Cactaceae **Part Two: *Echinocactus*** JANAS 29(1):13. 1995. (M. Chamberland)  
Cactaceae **Part Three: *Cylindropuntia*** JANAS 32(1):32. 1999. (D.J. Pinkava)  
Cactaceae **Part Four: *Grusonia*** JANAS 32(1):48. 1999. (D.J. Pinkava)  
Cactaceae **Part Five: *Pediocactus* and *Sclerocactus*** JANAS 33(1):9. 2001. (K.D. Heil and J.M. Porter)  
Cactaceae **Part Six: *Opuntia*** JANAS 35(2):137. 2003. (D.J. Pinkava).  
Callitrichaceae JANAS 29(1):15. 1995. (J. Ricketson)  
Campanulaceae  
Cannabaceae JANAS 32(1):53. 1999. (C.T. Mason, Jr.)  
Capparaceae (Fig. 8)  
Caprifoliaceae (Fig. 10)  
Caryophyllaceae (Fig. 10)  
Celastraceae JANAS 30(2):57. 1998. (J.W. Brasher)  
Ceratophyllaceae JANAS 29(1):17. 1995. (J. Ricketson)  
Chenopodiaceae (Fig. 9)  
Clusiaceae  
Commelinaceae JANAS 33(1):19. 2001. (R. Puente and R. Faden)  
Convolvulaceae JANAS 30(2):61. 1998. (D.F. Austin)  
Cornaceae  
Crassulaceae JANAS 27(2):190. 1994. (R. Moran)  
Crossosomataceae JANAS 26(1):7. 1992. (C. Mason)  
Cucurbitaceae CANOTIA 12:55-85. 2016. (M. Butterwick)  
Cupressaceae JANAS 27(2):195. 1994. (J. Bartel)  
Cuscutaceae  
Cyperaceae **Part One: Key to the Genera and *Carex***. CANOTIA 11(1):1. 2015. (G. Rink and M. Licher)  
Dennstaedtiaceae CANOTIA 4(2):38. 2008. (G. Yatskievych and M.D. Windham; Fig. 1)  
Dipsaceae JANAS 27(2):201. 1994. (J.E. LaFerriere)  
Dryopteridaceae (Fig. 1)  
Elaeagnaceae  
Elatinaceae  
Ephedraceae (Fig. 2)  
Ericaceae CANOTIA 4(2):21. 2008. (J.L. Anderson; Fig. 11)  
Euphorbiaceae **Part One: *Acalypha* and *Cnidioscolus*** JANAS 29(1):18. 1995. (G.A. Levin)  
Equisetaceae CANOTIA 4(2):41. 2008. (G. Yatskievych and M.D. Windham)  
Fabaceae **Part One: *Errazuria*, *Marina*, *Parryella*, and *Psorothamnus*** CANOTIA 7:1. 2011 (S. Rhodes, J. Beasley, and T. Ayers; Figs. 12–13)  
Fagaceae JANAS 27(2):203. 1994. (L.R. Landrum)  
Fouquieriaceae JANAS 32(1):55. 1999. (C.T. Mason, Jr.)  
Fumariaceae JANAS 33(1):27. 2001. (S. Holiday and A. Perez)  
Garryaceae JANAS 33(1):31. 2001. (R. Puente and T.F. Daniel)  
Gentianaceae JANAS 30(2):84. 1998. (C.T. Mason, Jr.)  
Geraniaceae (Fig. 14)  
Grossulariaceae  
Haloragaceae  
Hippuridaceae JANAS 29(1):25. 1995. (J. Ricketson)  
Hydrangeaceae  
Hydrocharitaceae CANOTIA 14: 22. 2018 (J.Ricketson)  
Hydrophyllaceae (Fig. 14)  
Iridaceae **Part One: *Sisyrinchium*** JANAS 27(2):215. 1994. (A.F. Cholewa and D.M. Henderson)  
Iridaceae **Part Two: *Iris* and *Nemastylis*** JANAS 33(1):35. 2001. (C.T. Mason, Jr.)  
Isoëtaceae CANOTIA 5(1):27. 2009. (G. Yatskievych and M.D. Windham)  
Juglandaceae JANAS 27(2):219. 1994. (J.E. LaFerriere)  
Juncaceae (Fig. 19)  
Juncaginaceae  
Key to Families of Vascular Plants in Arizona JANAS 35(2):88. 2003. (D.J. Keil)  
Krameriaceae JANAS 32(1):57. 1999. (B.B. Simpson and A. Salywon)  
Lamiaceae **Part One: *Agastache*, *Hyptis*, *Lamium*, *Leonurus*, *Marrubium*, *Monarda*, *Monardella*, *Nepeta*, *Salazaria*, *Stachys*, *Teucrium*, and *Trichostema*** JANAS 35(2):151. 2003. (C.M. Christy, D.Z. Damrel, A. Henry, A. Trauth- Nare,

R. Puente-Martinez, and G. Walters)  
**Lemnaceae** JANAS 26(1):10. 1992. (E. Landolt)  
**Lennoaceae** JANAS 27(2):220. 1994. (G. Yatskievych)  
**Lentibulariaceae** CANOTIA 8(2):54-58. 2012. (B. Rice)  
 Liliaceae (Fig. 19)  
 Linaceae  
**Loasaceae** JANAS 30(2):96. 1998. (C.M. Christy)  
 Lythraceae  
 Malpighiaceae  
**Malvaceae Part One: All genera except *Sphaeralcea*.**  
**JANAS 27(2):222. 1994. (P.A. Fryxell)**  
**Marsileaceae** CANOTIA 5(1):30. 2009. (G. Yatskievych  
 and M.D. Windham)  
**Martyniaceae** CANOTIA 3(2):26. 2007. (R. Gutierrez,  
 Jr.)  
 Meliaceae  
**Menispermaceae** JANAS 27(2):237. 1994. (J.E.  
 LaFerriere)  
**Menyanthaceae** JANAS 33(1):38. 2001. (C.T. Mason,  
 Jr.)  
**Monotropaceae** JANAS 26(1):15. 1992. (E. Haber)  
**Molluginaceae** JANAS 30(2):112. 1998. (C.M. Christy)  
 Moraceae  
**Najadaceae** CANOTIA 14:30. 2018 (J.Ricketson)  
 Nyctaginaceae (Fig. 14)  
**Nymphaeaceae** JANAS 29(1):26. 1995. (J. Ricketson)  
 Oleaceae (Fig. 15)  
 Onagraceae (Fig. 15)  
 Ophioglossaceae  
 Orchidaceae  
 Orobanchaceae  
**Oxalidaceae** JANAS 30(2):115. 1998. (R. Ornduff and  
 M. Denton)  
**Papaveraceae** JANAS 30(2):120. 1998. (G.B. Ownbey  
 with contributions by J.W. Brasher and C. Clark)  
**Passifloraceae** JANAS 33(1):41. 2001. (J.M.  
 MacDougal)  
**Phrymaceae** CANOTIA 12:1-21. 2016. (K. Hansen, E.  
 Johnson, K.O. Phillips, J. Talboom and T. Ayers)  
**Phytolaccaceae** JANAS 33(1):46. 2001. (V. Steinmann)  
 Pinaceae  
**Plantaginaceae** JANAS 32(1):62. 1999. (K.D. Huisinga  
 and T.J. Ayers)  
**Platanaceae** JANAS 27(2):238. 1994. (J.E. LaFerriere)  
 Plumbaginaceae  
 Poaceae (Fig. 20)  
**Polemoniaceae** CANOTIA 1:1. 2005. (D. Wilken and M.  
 Porter)  
 Polygalaceae  
 Polygonaceae (Fig. 15)  
**Polypodiaceae** CANOTIA 5(1):34. 2009. (G.  
 Yatskievych and M.D. Windham; Fig. 1)  
**Pontederiaceae** JANAS 30(2):133. 1998. (C.N. Horn)  
**Portulacaceae** CANOTIA 2(1):1. 2006. (A. Bair, M.  
 Howe, D. Roth, R. Taylor, T. Ayers, and R.W.  
 Kiger)  
 Potamogetonaceae  
**Primulaceae** JANAS 26(1):17. 1992. (A.F. Cholewa;  
 Fig. 16)  
**Psilotaceae** CANOTIA 3(2):32. 2007. (R. Gutierrez, Jr.)  
**Pyrolaceae** JANAS 26(1):22. 1992. (E. Haber)  
**Rafflesiaceae** JANAS 27(2):239. 1994. (G. Yatskievych)  
 Ranunculaceae (Fig.15)  
**Resedaceae** CANOTIA 14:35. 2018 (R.Gutierrez)  
**Rhamnaceae** CANOTIA 2(1):23. 2006. (K. Christie, M.  
 Currie, L. Smith Davis, M-E. Hill, S. Neal, and T.  
 Ayers)  
**Rosaceae Part One: *Rubus*.** JANAS 33(1):50. 2001.  
 (J.W. Brasher)  
**Rubiaceae** JANAS 29(1):29. 1995. (L. Dempster and

E.T. Terrell; Fig. 16)  
**Ruppiaceae** CANOTIA 14:38. 2018 (J. Ricketson)  
 Rutaceae  
**Salicaceae Part One: *Populus*.** JANAS 26(1):29. 1992.  
 (J.E. Eckenwalder)  
**Salicaceae Part Two: *Salix*.** JANAS 29(1):39. 1995.  
 (G.W. Argus)  
**Salviniaceae** CANOTIA 4(2):50. 2008. (G. Yatskievych  
 and M.D. Windham)  
**Santalaceae** JANAS 27(2):240. 1994. (J.E. LaFerriere)  
**Sapindaceae** JANAS 32(1):76. 1999. (A. Salywon)  
**Sapotaceae** JANAS 26(1):34. 1992. (L.R. Landrum)  
**Saururaceae** JANAS 32(1):83. 1999. (C.T. Mason, Jr.)  
**Saxifragaceae** JANAS 26(1):36. 1992. (P. Elvander; Fig.  
 16)  
**Scrophulariaceae** CANOTIA 14:41. 2018 (R.Crawford,  
 K.Noonan, and T.Ayers ) (see also Phrymaceae)  
**Selaginellaceae** CANOTIA 5(1):39. 2009. (G.  
 Yatskievych and M.D. Windham)  
**Simaroubaceae** JANAS 32(1):85. 1999. (J.W. Brasher)  
**Simmondsiaceae** JANAS 29(1):63. 1995. (J. Rebman)  
**Solanaceae Part One: *Datura*.** JANAS 33(1):58. 2001.  
 (R. Bye)  
**Solanaceae Part Two: Key to the Genera and *Solanum*.**  
**CANOTIA 5(1):1. 2009. (S.T. Bates, F. Farruggia,  
 E. Gilbert R. Gutierrez, D. Jenke, E. Makings, E.  
 Manton, D. Newton, and L.R. Landrum)**  
**Solanaceae Part Three: *Lycium*.** CANOTIA 5(1):17.  
 2009. (F. Chiang and L.R. Landrum)  
**Solanaceae Part Four: *Physalis* and *Quincula*.**  
**CANOTIA 9:1. 2013. (L.R. Landrum, A. Barber,  
 K. Barron, F.S. Coburn, K. Sanderford, and D.  
 Setaro)**  
**Solanaceae Part Five: *Chamaesaracha*.** CANOTIA 9:13.  
 2013. (E. Manton)  
**Solanaceae Part Six: *Nicotiana*.** CANOTIA 14:54. 2018.  
 (E.Makings and J.P.Solves)  
**Sparganiaceae** JANAS 33(1):65. 2001. (J. Ricketson)  
 Sterculiaceae  
 Tamaricaceae  
**Thelypteridaceae** CANOTIA 5(1):49. 2009. (G.  
 Yatskievych and M.D. Windham)  
 Tiliaceae  
**Typhaceae** JANAS 33(1):69. 2001. (J. Ricketson)  
**Ulmaceae** JANAS 35(2):170. 2003. (J.W. Brasher)  
**Urticaceae** JANAS 26(1):42. 1992. (D. Boufford)  
 Valerianaceae  
 Verbenaceae  
**Violaceae.** JANAS 33(1):73. 2001. (R.J. Little; Fig. 17)  
**Viscaceae** JANAS 27(2):241. 1994. (F.G. Hawksworth  
 and D. Wiens)  
 Vitaceae  
**Zannichelliaceae** CANOTIA 14:63. (J. Ricketson)  
 Zygophyllaceae (Fig. 17)